OCCASIONAL PAPERS

of the

MUSEUM OF NATURAL HISTORY
The University of Kansas
Lawrence, Kansas

NUMBER 35, PAGES 1-51 APRIL 16, 1975

A REVIEW OF THE ANDEAN LEPTODACTYLID FROG GENUS *PHRYNOPUS*

By

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In 1932 Hampton Parker described *Eupsophus wettsteini* from the Peruvian Andes. In discussing the systematic position of this species he pointed out the then ominous possibility that *Eleutherodactylus, Eupsophus,* and *Syrrhophus* might eventually be merged into a single genus. Parker envisioned a "*Borborocoetes*" group of *Eleutherodactylus* as having given rise to the annectant *Syrrhopus simonsii, S. festae,* and *Eupsophus wettsteini,* and that this complex of species had given rise to the more southern *Eupsophus* (especially *E. peruanus*). Although he separated the species into two genera, Parker evidently viewed them as an annectant generic group. Subsequently, these three species and several others were gathered into the genus *Niceforonia* (Lynch 1971).

Lynch (1971) recognized ten genera of leptodactylids in the tribe Eleutherodactylinii (Telmatobiinae). Four of the genera (*Eleutherodactylus, Sminthillus, Syrrhophus,* and *Tomodactylus*) were characterized, in part, by the possession of digital discs and the associated T-shaped terminal phalanges. The other six genera (*Amblyphrynus, Euparkerella, Holoaden, Hylactophryne, Ischnocnema* and *Niceforonia*) do not have digital discs and with the exception of *Euparkerella* (which has complex terminal phalanges) have knobbed terminal phalanges.

Only three eleutherodactyline genera have species represented in the Andean frog fauna at elevations above 2000 meters. The genus *Amblyphrynus* is represented by a single species in Andean

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Colombia. Frogs of this genus have broad heads (head width 50–60 % SVL) and simple digits (no pads or discs; terminal phalanges knobbed). The genus *Eleutherodactylus* is represented by many species in the Colombian and Ecuadorian Andes and few species elsewhere. These frogs have heads of normal width (HW 30–42% SVL) and complex digits (discs on narrowly to broadly dilated pads; terminal phalanges T–shaped).

A third supraspecific group is represented by at least two Colombian, three Ecuadorian, eight Peruvian, and one Bolivian species. These frogs have heads of normal breadth and simple digits; included among the fourteen species are the type–species of the nominal genera *Niceforonia* Goin and Cochran, 1963, *Noblella* Barbour, 1930, and *Phrynopus* Peters, 1874. I consider the fourteen species congeneric and a distinct generic entity; accordingly, *Niceforonia* and *Noblella* are here relegated to the synonymy of *Phrynopus*.

In recent years, *Niceforonia* has been applied to some of the nominate species of *Phrynopus*. Since 1932, *Phrynopus peruanus* Peters has been considered a species of *Eupsophus* (Parker, 1932) and since 1971 the type–species of *Noblella* has been considered a species of *Eleutherodactylus* (Lynch, 1971). *Phrynopus peruanus* and *Niceforonia nana* so closely resemble one another that their congeneric status cannot be seriously questioned. The third type–species (*Noblella peruviana*) is more distinctive and is treated separately below.

Presently, ten names are applied to the species of *Phrynopus* (nine are listed as *Niceforonia* by Lynch, 1971). One of the names (*N. festae* Peracca) was incorrectly applied to the species of *Phrynopus* found in the upper Papallacta valley in Napo Province, Ecuador by Lynch (1968).

Considerable material of this genus has accumulated since my 1968 paper; that material requires the recognition of four previously unknown species and enables me to review the genus as an entity and to discuss the variation in osteological character–states seen among the species of the genus. Two hundred and eighty–two specimens including 17 cleared and stained skeletons were studied.

ACKNOWLEDGMENTS

For loan of species or provision of working space at their respective institutions, I am indebted to José M. Cei, the late Doris M. Cochran, William E. Duellman, Josef Eiselt, Alice C. G. Grandison, Arnold G. Kluge, the late James A. Peters, Douglas Rossman, Richard Thomas, Charles F. Walker, Ernest E. Williams, George Zug, and Richard G. Zweifel.

Field work in Ecuador was supported by grants from the Committee on Systematic and Evolutionary Biology, The University of Kansas, Sigma Xi, and the Watkins Fund of the Museum of Natural

History, The University of Kansas. Travel to museums was supported by the University of Kansas Graduate School during my tenure as an Honors Fellow (1966–69) and The University of Nebraska Research Council. Robert Henderson and Marsha Lynch aided me in the field and William E. Duellman and Thomas H. Fritts provided detailed field notes and additional information about localities and the organisms they had collected. Todd Georgi aided in histological study of the pectoral girdle. The aid of all these persons has substantially contributed to my study of these frogs.

Abbreviations for collections used throughout the text are:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
IBM/UNC	Instituto de Biologia, Mendoza–Universidad Nacional de Cuyo
KU	The University of Kansas Museum of Natural History
LSUMZ	Louisiana State University Museum of Zoology
MCZ	Museum of Comparative Zoology
MNW	Naturhistorisches Museum zu Wien
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum (National Museum of Natural History)
WCAB	Private collection of Werner C. A. Bokermann, São Paulo.

STRUCTURE OF THE DIGITS

Eleutherodactylus is a large and diverse genus; against this background of morphological diversity, *Phrynopus* can be distinguished, at present, only on the basis of the structure of the digits. The majority of *Eleutherodactylus* species have dilated digital pads (bearing discs on their ventral surface) supported internally by distinctly T-shaped terminal phalanges. The disc is a distinct structure on the ventral surface of the digit and is defined by a circumferential groove (Fig. 1). In most species having apical dilation of the digit, the pad is wider than long and the dilation ratio (pad width/digit width below pad) is 2.0–3.5. This value is lowest when the digits bear lateral fringes (as in *E. riveti*). Several *Eleutherodactylus* species have narrow digits, that is, the pad is longer than wide or the length and width are equal; the dilation ratio is as low as 1.2–1.3. The narrow-toed *Eleutherodactylus* include those with narrow finger and narrow toe pads (*e.g., E. binotatus, E. cornutus, E. elassodiscus, E. octavioi,* and several others) as well as those with narrow finger pads and broad toe pads (*e.g., E. anomalus*). In most of the narrow-toed species, the terminal phalanges of the fingers are more knobbed (as contrasted to T-shaped) whereas those of the toes are more T-shaped (Lynch, 1971). The

most proximal digits (I and sometimes II of the hand; I and II of the foot) may not bear discs (*i.e.*, no circumferential groove present) but the more distal digits always bear discs, even in the most narrow-toed species (*e.g., E. elassodiscus, E. nigrovittatus,* and *E. octavioi;* Fig. 1).

The simple-toed Andean frogs of the genus *Phrynopus* do not have digital discs (Fig. 1). There is apical swelling (= bulbing) of the digit in some of these frogs and dilation ratios of 1.0–1.2. Earlier (1971), I characterized this genus (as *Niceforonia*) as having knobbed terminal phalanges. However, some of the Peruvian taxa have lateral processes on the terminal phalanges (Fig. 2) that are intermediate in size between the T-shaped terminal phalanges of some of the narrow-toed *Eleutherodactylus* and the knobbed character-state seen in *Phrynopus peraccai, P. flavomaculatus,* and *P. montium.*

The annectant condition seen in some Peruvian species (no discs,

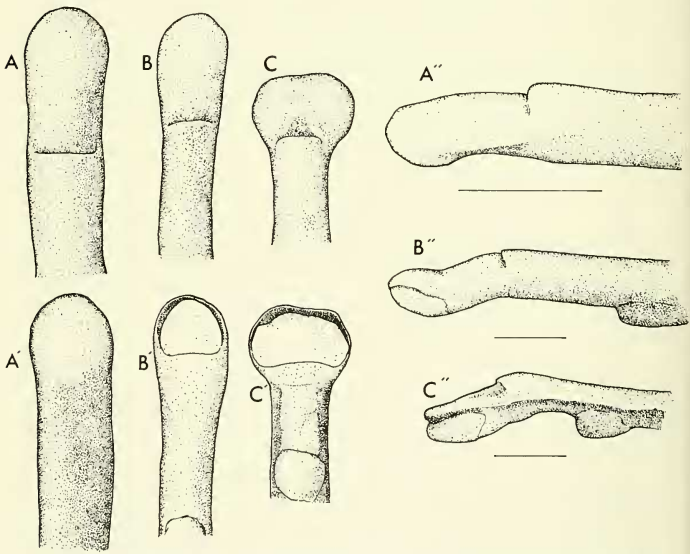

Fig. 1.—Dorsal views of distal portion of (A) fourth toe, left foot, *Phrynopus peruvianus,* (B) fourth toe, left foot, *Eleutherodactylus elassodiscus,* (C) fourth finger, left hand, *E. riveti.* Ventral views of same digits, (A′) *P. peruvianus,* (B′) *E. elassodiscus,* (C′) *E. riveti.* Lateral views of same digits, (A″) *P. peruvianus,* (B″) *E. elassodiscus,* (C″) *E. riveti. Phrynopus peruvianus,* KU 138959; *Eleutherodactylus elassodiscus,* WCAB 37915; *E. riveti,* KU 120060. Lines below lateral views equal 1 mm.

rudimentary or vestigal T-shaped terminal phalanges) could be used as evidence for combining several of the simple-toed genera of eluthérodactylines with *Eleutherodactylus* as once noted by Parker (1932). To do so, however, does not simplify or improve leptodactylid taxonomy. Although the phalangeal characteristic is no longer diagnostic, the digital disc characteristic remains diagnostic; accordingly, I prefer to retain the simple-toed genera as distinct from *Eleutherodactylus*.

THE STATUS OF *NOBLELLA* BARBOUR

Noble (1921) named *Sminthillus peruvianus* on the basis of five specimens from Juliaca, Puno, Perú. The species was designated the type-species of *Noblella* by Barbour (1930), who neither diagnosed nor defined the genus. Lynch (1971), following study of a partially macerated, cleared and stained paratype of *peruviana*, placed it in the genus *Eleutherodactylus* largely because a single T-shaped terminal phalange was found among the fragments of the skeletal preparation.

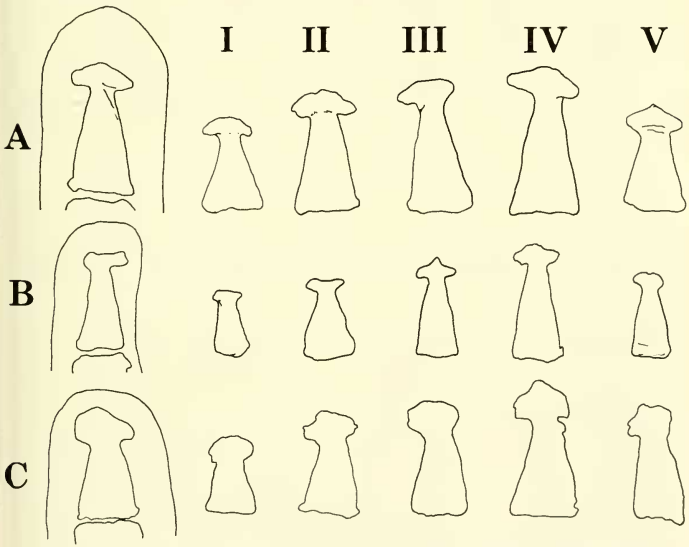

FIG. 2.—Terminal phalanges of *Phrynopus parkeri* (Row A, KU 135306), *P. peruvianus* (Row B, figure at far left, KU 138928; other five phalanges of KU 138926), and *P. cophites* (Row C, KU 138909). Column to left (no roman numeral) is of third finger. The five columns headed by roman numerals include terminal phalanges on toes I through V.

Collections made in southern Perú by William E. Duellman and Thomas H. Fritts include a large series of adults and subadults of a simple-toed eleutherodactyline frog. Comparison of the smallest of these with the holotype of *Sminthillus peruviana* convinced me that they are conspecific. Alizarin-Red preparations of adults of the frog revealed that the terminal phalanges are roughly T-shaped (Fig. 2) even though the digit tips are simple (Fig. 1). Noble (1921) assigned the species to *Sminthillus* and the Brachycephalidae because the pectoral girdle is arcifero-firmisternal in the sense of Boulenger and Cope. Griffiths (1959) argued that the girdle architecture is arciferal in the sense that he diagnosed the character-state; the adult specimens are functionally firmisternal in that the halves of the epicoracoid cartilages are fused (Fig. 3) but are anatomically arciferal as in all other leptodactylid frogs. The clavicles are oriented at approximately right angles to the sagittal plane in contrast to the strongly curved clavicles seen in other species of the genus *Phrynopus*.

Character-states for the characteristics used in my generic review of the leptodactylids (Lynch 1971) are listed below for *Noblella peruviana:* sternum, a cartilaginous plate; omosternum present, relatively small and elongate; eight procoelous presacral vertebrae, non-imbricate; cervical vertebra with widely separated cotyles, not fused to second vertebra; sacral diapophyses rounded, deflected posteriorly; sacro-coccygeal articulation bicondylar; vertebral shield lacking; transverse processes of vertebrae three to eight about as long as sacral diapophyses or slightly shorter; cranial bones not exostosed or dermostosed; maxillary arch complete; maxilla and premaxilla toothed, teeth blunt, pedicellate; palatal shelf of premaxilla broad, weakly incised; facial lobe of maxilla relatively shallow; nasals small, median separation moderate; frontoparietals complete, fontanelle not exposed, not ornamented; frontoparietal not fused to prootic, epiotic eminences obsolete; cristae paroticae short, broad; occipital artery passes dorsal to skull bones; zygomatic ramus of squamosal short, widely separated from maxillary arch; otic ramus of squamosal short, otic plate narrow; plectrum (columella) present; prevomers small, edentate, dentigerous rami lost; sphenethmoid entirely ossified, large, extending anteriorly to middle of nasals; anterior ramus of parasphenoid short, broad, not keeled; parasphenoid alae oriented at right angles to anterior ramus, widely separated from short, median rami of pterygoids; pterygoids moderately large, anterior rami extending nearly to palatines; occipital condyles small, stalked, widely separated; mandibles lacking odontoids; phalangeal formulae 2-2-3-3, 2-2-3-4-3; terminal phalanges bear short, irregular-shaped lateral processes; digits bulbous apically, lacking discs; alary processes of hyoid plate on narrow stalks; *m. sternohyoideus* and *m. petrohyoideus anterior* insert on lateral edges of hyoid plate; pupil horizontal; males with median subgular

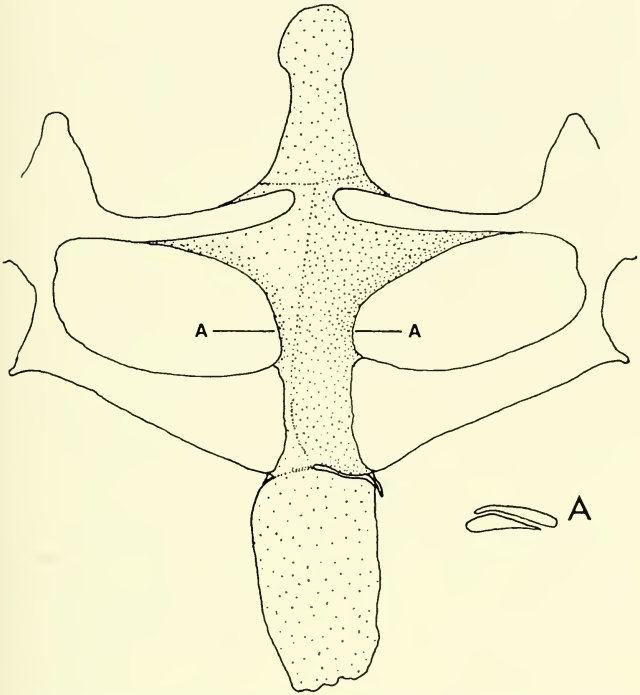

FIG. 3.—Ventral view of pectoral girdle of *Phrynopus peruvianus*. Cartilage is stippled. (A) Cross-section through epicoracoidal bridge at Point A—A.

vocal sac; toes not webbed, no lateral fringes; two metatarsal tubercles present; eggs large, not pigmented, few in number; males lacking nuptial asperities.

The type-species of *Niceforonia* and *Phrynopus* differ from one another in skin texture (venter areolate in *N. nana*), condition of the ear (plectrum, cavum tympanicum, and tympanic annulus absent in *N. nana*), and in coloration, proportions, and some details of foot structure. They are similar in having widely separated cervical cotyles (and occipital condyles), in having the frontoparietals complete (fontanelle not exposed), in having prevomerine odontophores (bearing teeth) situated well posterior to the choanae, in having simple digits, and in having "normal" arciferal pectoral girdles.

The type-species of *Noblella* differs from the type-species of

Niceforonia and *Phrynopus* in some trivial features but also in lacking prevomerine odontophores and teeth (as well as much of the prevomers) and in having a pseudofirmisternal pectoral girdle (epicoracoid cartilages partially fused; clavicles straight and at right angles to sagittal plane). The absence of prevomerine odontophores and teeth in *peruvianus* is not an especially significant trait insofar as generic distinction is concerned. Five other Bolivian and Peruvian species also lack prevomerine odontophores. However in these frogs the dentigerous ramus of the prevomer has not been lost.

Thus, the only trait supporting a generic separation is the architecture of the pectoral girdle. In the absence of corroborative distinctions, I am unwilling to advocate separation of *Noblella* and *Phrynopus*.

With two exceptions, the original descriptions of the named species are based on adults. Werner's (1899) description of *columbianus* is very brief and no specimens have been identified since the original description. Noble's (1921) description of *peruvianus* is incomplete in that it was based on juveniles. The acquisition of a large sample of adults enables a redescription of the type-species of *Noblella*.

SYSTEMATIC ACCOUNTS

The material available for seven of the species is too limited to warrant a revision of the genus. The published descriptions of *P. flavomaculatus* (Parker), *P. laplacai* (Cei), *P. montium* (Shreve), and *P. wettsteini* (Parker) are considered adequate for future identification of samples when the diagnoses presented here are considered. I therefore present species descriptions for only the new species and for *P. peruanus* Peters, *P. peruvianus* (Noble) and *P. simonsii* (Boulenger).

Phrynopus Peters

Phrynopus Peters 1874:416 (Type-species by monotypy, *Phrynopus peruanus* Peters, 1874).

Noblella Barbour 1930:81 (Type-species by original designation, *Sminthillus peruvianus* Noble, 1921). New synonymy.

Niceforonia Goin and Cochran 1963:499. (Type-species by original designation, *Niceforonia nana* Goin and Cochran, 1963). New synonymy.

Diagnosis.—Eleutherodactyline telmatobiine frogs with simple digital tips, digits neither greatly shortened nor elongated, plantar surfaces lacking conical or subconical supernumerary tubercles, having alary processes on the hyoid plate, and having a "normal" skull architecture (*i.e.*, not helmeted), and normal head width (HW/SVL = 31.1–40.8%).

Content.—Fourteen species: *P. brunneus* new species, *P. columbianus* (Werner), *P. cophites* new species, *P. flavomaculatus* (Parker), *P. laplacai* (Cei), *P. montium* (Shreve), *P. nanus* (Goin and Cochran), *P. parkeri* new species, *P. peraccai* new species, *P. pereger* new species, *P. peruanus* Peters, *P. peruvianus* (Noble), *P. simonsii* (Boulenger), and *P. wettsteini* (Parker).

Description.—In dorsal view the snout is either rounded or

weakly acuminate. In lateral profile, the snout is sloping in *flavomaculatus* and *parkeri* (Fig. 4) whereas it is rounded or truncate in the other twelve species. The canthus rostralis is sharp and concave in all species except *brunneus* and *peraccai* which have rounded canthi. The interorbital space is flat and cranial crests lacking in all species except *flavomaculatus.* Three species (*cophites, nanus,* and *simonsii*) are earless; the remaining eleven species have complete ears although the tympana are concealed in *laplacai, montium, parkeri, peraccai, pereger, peruvianus,* and *wettsteini;* six species lack prevomerine teeth and odontophores; *peruvianus* lacks the dentigerous processes of the prevomers; *cophites, laplacai, montium,* and *wettsteini* have long thin dentigerous processes but lack odontophores; *simonsii* has large prevomers but lacks the odontophores; the other eight species have prevomerine teeth and associated processes. The dentigerous processes lie posterior and median to the choanae. In those species for which males are available, vocal sacs and slits are absent in *brunneus* and *cophites.* Males are not known for *columbianus, nanus, peraccai,* or *simonsii.*

The skin of the dorsum and venter is smooth in *brunneus, flavomaculatus, parkeri, peraccai, pereger, peruanus,* and *peruvianus;* the skin of the dorsum is weakly to coarsely areolate and that of the venter coarsely areolate in *cophites, laplacai, montium, nanus, simonsii,* and *wettsteini.* Werner (1899) made no direct statements about skin texture in *columbianus,* but because he compared his frog with *Ischnocnema quixensis,* I conclude that *columbianus* had smooth skin on the venter and a somewhat warty dorsum. Dorsolateral folds are present in only *simonsii.*

The limbs of all species are short and robust. The limbs are shortest in *cophites* (shank about 32% SVL) and longest in *flavomaculatus* (shank about 50% SVL). No species has axillary patagia. The fingers and toes are of moderate length (Figs. 5–7) and lack discs although the digital tips may be weakly swollen (perhaps due to preservation). The subarticular tubercles are flat, round, and simple. Most species have three palmar tubercles (innermost is the thenar tubercle); the outer palmar tubercle is absent (probably fused to median) in *brunneus, cophites, laplacai,* and *peruvianus.* The thumb is longer than the second finger in *brunneus, flavomaculatus, laplacai, parkeri, peraccai, pereger,* and *peruvianus* (Figs. 5, 6a, 7b), the thumb is equal in length to the second finger in *columbianus* (*fide* Werner, 1899), and the thumb is shorter than the second finger in *cophites, montium, nanus, peruanus, simonsii,* and *wettsteini* (Figs. 6b, 7a).

Werner (1899) reported a single metatarsal tubercle in *columbianus;* all other taxa have two. Both metatarsal tubercles are large and subequal in size in *cophites, flavomaculatus, laplacai, parkeri, peraccai, pereger, peruanus, peruvianus,* and *simonsii* (Figs. 6c, 8). The inner metatarsal tubercle is about twice the size of the outer

in *brunneus, montium, nanus,* and *wettsteini.* Most species lack lateral fringes on the toes and basal webbing, but both features are seen in *nanus* and *simonsii* (webbing does not enclose basal subarticular tubercles).

Males, where known, are smaller than females. The smallest species are *nanus* (a single female 20.5 mm SVL) and *peraccai* (17 females, 18.4–20.6 mm SVL). The largest species are *flavomaculatus* (14 females, 34.8–42.6 mm SVL) and *parkeri* (10 females, 27.4–35.0 mm SVL).

Osteology.—Cleared and stained skeletal specimens (see specimens examined) are available for nine of the fourteen species (*cophites, flavomaculatus, laplacai, montium, parkeri, peraccai, pereger, peruvianus,* and *wettsteini*). Limited osteological data were obtained through dissection of *brunneus* (USNM 192911, paratype), *peruanus* (UMMZ 89477), and *simonsii* (BMNH 1947.2.15.43, lectotype). Aside from externally visible traits, no osteological data are available for the Colombian species (*columbianus* and *nanus*), and the discussion of osteological features accordingly excludes them.

The skulls of *Phrynopus* species are broader than long or as broad as long. The maxillary arch does not extend posterior to the occipital region. The skulls are about one-half as high as long (not greatly flattened or conspicuously vaulted). The maxillary arch is complete and the premaxillae and maxillae bear blunt, pedicellate teeth. The brain case appears narrow in *brunneus, flavomaculatus* (Fig. 9), *parkeri* (Fig. 10), and *pereger* because the edges of the frontoparietals are approximately parallel whereas the edges diverge posteriorly in the other species (Fig. 11, 12). The columellae are lost in *cophites* and *simonsii* (and *nanus*); no other bones have been lost in the species of the genus. Exostosis of cranial elements occurs only in *flavomaculatus* (Fig. 9) although some rugosity at the edges of the frontoparietals is seen in *montium* (Lynch, 1971) and *peraccai* (identified as *festae* in Lynch, 1968). Cranial dermostosis is not known in the genus.

The alary processes of the premaxillae are relatively broad at their bases and directed dorsally in species with rounded or truncate snouts or posterodorsally in species with sloping snouts (*flavomaculatus* and *parkeri*). The premaxillary palatal shelf is broad and only weakly dissected in *cophites* and *peruvianus* (Figs. 11–12). The palatal process in these species is slightly longer than the maxillary process. The premaxillary palatal shelf of *laplacai* is slightly more dissected; the palatal process is prominent and longer than the maxillary process. The premaxillary palatal shelf in *brunneus, flavomaculatus, parkeri* (Fig. 10), *peraccai, pereger, peruanus,* and *wettsteini* is deeply dissected and the palatal and maxillary processes subequal in length. In *montium* (Lynch, 1971: Fig. 104), the palatal and maxillary processes are greatly elongated and the dissection of the palatal shelf greater.

The nasals are widely separated and relatively small in *montium*, *peruanus*, and *peruvianus* (Fig. 11). The nasals are less widely separated and slightly larger in *cophites* (Fig. 12) and *peraccai*. The nasals are narrowly separated and large in *laplacai*, *simonsii*, and *wettsteini*, and in contact and large in *brunneus*, *flavomaculatus* (Fig. 9), *parkeri* (Fig. 10), and *pereger* . The nasals of all species have elongate maxillary processes that are narrowly separated from or in tenuous contact with the *pars facialis* of the maxillae. The nasals are narrowly separated from the frontoparietals in *brunneus*, *flavomaculatus*, *parkeri* (Figs. 9–10), and *pereger*, but widely separated in the other species examined (Figs. 11–12).

The frontoparietals are in median contact in all species except *cophites* which has a moderate-sized frontoparietal fontanelle (Fig. 12). The lateral edges of the frontoparietals frequently bear small bony ridges or weak exostosis (*montium*, *peraccai*, and *wettsteini*) which are not detectable externally. The frontoparietals are heavily exostosed and bear prominent lateral crests in *flavomaculatus* (Fig. 9). The frontoparietals are not fused to the prootics in any specimen examined.

The cristae paroticae are elongate and narrow in *flavomaculatus*, a large species (Fig. 9), short and stocky in *cophites* (Fig. 12), *laplacai*, *montium*, *peruvianus* (Fig. 11), *peraccai*, and *wettsteini*, small species, and of intermediate length and robustness in *parkeri* (Fig. 10) and *pereger*, frogs of intermediate size. Length and breadth of the cristae paroticae appear correlated with body size, at least in *Phrynopus*. The epiotic eminesces are most prominent in *flavomaculatus* and *parkeri* and obsolete in the other species. The occipital condyles are widely separated in all species and weakly stalked (not stalked in *cophites* or *peruvianus*).

The squamosals have broad otic plates resting on the cristae paroticae in *flavomaculatus*, *parkeri* (Figs. 9–10) and *pereger*, or narrow otic plates not resting on the cristae paroticae (*cophites*, *laplacai*, *montium*, *peraccai*, *peruvianus*, and *wettsteini*). The zygomatic and otic rami of the squamosals are of equal length and the squamosomaxillary angles 50–55°. The squamosal does not contact the maxilla.

The maxillary palatal shelf is broadest anteriorly and narrows posteriorly. The palatal shelf tapers gradually to the end of the dentigerous series and the point at which the pterygoid contacts the maxilla; at this point the shelf abruptly narrows (Figs. 10, 12). In *peruvianus* the shelf tapers gradually through the point of maxillary–pterygoid contact (Fig. 11).

The sphenethmoid is very large in *peraccai* (calcified or ossified to a point anterior to the nasals) and relatively small in *cophites* (Fig. 12; calcified portion does not reach the nasals). The sphenethmoid is of intermediate size in the other species (Fig. 11).

Prevomerine teeth are present on prominent dentigerous proc-

esses in *brunneus, columbianus* (fide Werner), *flavomaculatus, nanus, parkeri* (Fig. 10), *peraccai, pereger,* and *peruanus.* The prevomer is edentate and lacks the dentigerous processes in *cophites, laplacai, montium, peruvianus, simonsii,* and *wettsteini* (Figs. 11–12). The prevomers are separated in all species examined. The choanal and dentigerous rami of the prevomer are large in *flavomaculatus, parkeri* (Fig. 10), *peraccai, pereger,* and *simonsii.* The choanal ramus is large and the dentigerous ramus thin in *cophites* (Fig. 12), *laplacai, montium, peruanus,* and *wettsteini.* The dentigerous ramus is lost and the choanal ramus reduced to an irregular–shaped bone anteromedial to the choana in *peruvianus* (Fig. 11).

Palatines are present and well developed in all species. The anterior ramus of the parasphenoid contacts the palatines and prevomers in *brunneus, flavomaculatus, parkeri* (Fig. 10), *pereger,* and *simonsii.* The parasphenoid is slightly shorter in *laplacai* and *peraccai* and does not contact the palatines or prevomers. In *cophites* (Fig. 12), *montium, peruanus, peruvianus* (Fig. 11), and *wettsteini,* the parasphenoid is much shorter and widely separated from the palatines. The alary processes of the parasphenoid are oriented at right angles to the anterior ramus in all species except for a slight posterior deflection in *flavomaculatus, parkeri* (Fig. 10) and *pereger.* The alary processes are shortest in *cophites* (Fig. 12). The median ramus of the pterygoid is in contact with the alary process (or overlaps it) in *brunneus, flavomaculatus, parkeri* (Fig. 10), and *pereger.* The two elements are narrowly separated in *montium* and *peraccai* and widely separated in *cophites* (Fig. 12), *laplacai, peruanus, peruvianus* (Fig. 11), and *wettsteini.* The pterygoids are more massive elements in *flavomaculatus* and *parkeri* than in the other species.

Three species (*cophites, nanus,* and *simonsii*) lack the plectrum, tympanic annulus, and cavum tympanicum; the other eleven species have complete ears although the ears may not be visible externally.

All species have eight procoelous presacral vertebrae. The transverse processes of the third and fourth vertebrae are longer than those of the second and fifth through eighth vertebrae. The transverse processes of vertebrae 5–8 are shorter than the sacral diapophyses of all species, but are shortest in *cophites, laplacai, montium, peruvianus,* and *wettsteini.* The sacral diapophyses are weakly dilated and deflected posteriorly. The sacrococcygeal articulation in bicondylar, and the coccyx lacks transverse processes. The ilia are of the leptodactyline type (Lynch, 1971). The limb bones lack flanges and vary from long and thin (*flavomaculatus*) to short and stocky (*cophites*).

All species have cartilaginous omosterna and sterna although the degree of calcification varies with the size of individuals. The omosternum is elongate and somewhat dilated anteriorly. The sternum is broad and weakly to markedly indented posteriorly (Cei,

1968; Peters, 1874; Fig. 13). I have not found the posterior indentations of the sterna of *laplacai, montium,* and *peruanus* as marked as figured by Cei (1968) and Peters (1874). The sternum is much narrower and not indented in *peruvianus* (Fig. 3). In all species except *peruvianus,* the clavicles are well-developed, thin, and moderately curved (Fig. 13). The epicoracoid cartilages broadly overlap and are loosely attached. The attachment of the epicoracoid cartilages is strongest anteriorly but the girdles are functionally arciferal. The coracoids are much shorter and stockier than the clavicles.

In *peruvianus,* the epicoracoid cartilages overlap more narrowly than in other *Phrynopus* (compare Figs. 3 and 13) and are more firmly attached to one another. The girdle of *peruvianus* is functionally firmisternal (pulling laterally on the forearms results in no displacement of the epicoracoid cartilages). Noble's specimens of *peruvianus* are all smaller than the recent material; he recorded partial firmisterny for his small frogs but the smallest of the recently collected specimens (which are larger than any of the types) is equally firmisternal as the largest. The fusion of the epicoracoid cartilages does not obscure the edges of the cartilages (Fig. 3). The two cartilages are not fused in the posterior one-half of the epicoracoid overlap but are tightly bound with connective tissue. Unlike the more typically arciferal species of *Phrynopus* and more like a ranoid type of pectoral girdle, the clavicles and coracoids of *peruvianus* are subequal in width and the clavicles are straight and oriented at more nearly right angles to the sagittal plane. In spite of the firmisternal modifications of the girdle, the arciferal condition (*sensu* Griffiths, 1959) of the girdle is demonstrated by the presence of epicoracoid horns and the overlapping and only partially fused epicoracoid cartilages (visible in serial sections of the epicoracoid bridge).

The phalangeal formulae are 2–2–3–3, 2–2–3–4–3 in all species and the stubbyness or slenderness of the digits is reflected in the shapes of the phalangeal bones. Several of the species have lateral processes on the terminal phalanges. The terminal phalanges are knobbed in *brunneus, flavomaculatus, laplacai, peraccai,* and *wettsteini,* whereas those of *cophites, parkeri, pereger, peruvianus,* and *simonsii* bear short, irregularly shaped lateral processes (Fig. 2). The lateral processes are better developed on the toes than on the fingers. Among species of *Eleutherodactylus,* the most poorly developed T-shaped terminal phalanges are found on the fingers of some species of the *binotatus* and *fitzingeri* groups (*binotatus, cruralis, granulosus, nigrovittatus,* and *octavioi*). The terminal phalanges of the fingers of these species match the weak lateral processes seen on the digits of *Phrynopus* (*cophites, parkeri, peruvianus,* and *simonsii*).

KEY TO SPECIES OF *PHRYNOPUS*

1. Prevomerine dentigerous processes present 2
   Prevomerine teeth and dentigerous processes absent 9
2. Skin of venter smooth 3
   Skin of venter areolate ..... *nanus*
3. Tympanum concealed ..... *parkeri*
   Tympanum visible 4
4. Cranial crests present ..... *flavomaculatus*
   Cranial crests absent 5
5. Outer metatarsal tubercle less than one–half size of inner 6
   Outer metatarsal tubercle more than one–half size of inner (usually equal in size) 7
6. Toes basally webbed; venter off–white ..... *columbianus*
   Toes not basally webbed; venter brown ..... *brunneus*
7. First finger shorter than second ..... *peruanus*
   First finger longer than second 8
8. Small frogs (♀ ♀ 19.0–21.7 mm SVL); shank less than 40% SVL; venter uniform brown ..... *peraccai*
   Larger frogs (♀ ♀ 24.0–31.8 mm SVL); shank more than 39% SVL; venter usually spotted ..... *pereger*
9. Tympanum absent 10
   Tympanum present, visible or concealed beneath skin 11
10. Toes bearing lateral fringes ..... *simonsii*
    Toes lacking lateral fringes ..... *cophites*
11. Skin of venter smooth 12
    Skin of venter aerolate 13
12. Inner tarsal tubercle present ..... *peruvianus*
    No tubercle on tarsus ..... *peruanus**
13. First finger shorter than second 14
    First finger as long as or longer than second ..... *laplacai*
14. Throat black or dark brown ..... *wettsteini*
    Throat not distinctly darker than venter ..... *montium*

ACCOUNTS OF SPECIES

In the following accounts I have presented species descriptions only in the cases of new species or in the cases where extensive additional material is available or where the original description was misleading through brevity. A diagnosis, a skeletal synonymy, and a section for miscellaneous remarks is presented for each taxon.

Phrynopus brunneus new species

Holotype.—USNM 192909, an adult male from 10 km WNW El Carmelo (= Pun), Carchi Prov., Ecuador, 3150m, collected 30 June 1962 by James A. Peters.

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* In some *peruanus*, the prevomerine odontophores are concealed beneath the tissue of the palate; such individuals would key out here.

Paratypes.—(3) USNM 192910–12, collected syntopically with the holotype.

Diagnosis.—A moderate-sized *Phrynopus* (3 ♂♂ 25.8–27.6 mm, one ♀ 29.6 mm SVL); skin of dorsum and venter smooth; first finger longer than second; fingers and toes not dilated at tips; toes lacking lateral fringes and basal webbing; two metatarsal tubercles, inner much larger than outer; tarsus lacking tubercles or folds; tympanum present, visible externally, one-half eye length in males, one-third eye length in single female; snout rounded in lateral profile; males lacking vocal sac and slits; prevomerine teeth present on prominent dentigerous processes lying median and posterior to choanae; frontoparietals complete, no crests; nasals moderately large, narrowly separated; anterior ramus of parasphenoid long, in contact with palatines; median ramus of pterygoid in contact with parasphenoid alae; body brown with indistinct darker mottling.

Description.—Head narrower than body, head wider than long; head width 34.3–37.9 ($\bar{x}$ = 36.8) % SVL; snout round in dorsal view, rounded in lateral profile (Fig. 4); snout short, eye length 1½ times E–N (eye–nostril distance); canthus rostralis round, somewhat concave; loreal region concave, sloping gradually to lips; lips not flared; nostrils directed dorsolaterally, not protuberant; interorbital region weakly furrowed, no cranial crests; upper eyelid width 78.7–93.5 ($\bar{x}$ = 86.7) % IOD (interorbital distance); supratympanic fold thick, prominent, concealing upper edge of tympanum; tympanum visible, round in males, higher than long in females, its horizontal diameter 43.1–47.8 ($\bar{x}$ = 45.8) % eye length in males, 30.3 in single females; males lacking vocal sac and slits; tongue large, about as long as wide, not notched posteriorly, posterior one-third not adherent to floor of mouth; choanae small, wider than long, not concealed by palatal shelf of maxillae; prevomerine dentigerous processes present, median and posterior to choanae, each process bearing a transverse row of 4–5 teeth; prevomerine dentigerous processes three to four times as wide as a choana.

Skin of dorsum and venter smooth except for weak areolations along lower flanks, posterior parts of undersides of thighs, and near anus; no dorsolateral folds; discoidal folds obscure, ending anterior to groin; no tubercles on eyelids; forearm lacking ulnar tubercles or folds; palmar tubercle bifid and larger than thenar tubercle; thenar surfaces bearing a few ill-defined supernumerary tubercles; subarticular tubercles large, round, simple, non-conical; fingers not fringed; first finger distinctly longer than second; digit tips round, not bulbous.

Tarsus and heel lacking tubercles or folds; two metatarsal tubercles, inner twice as long as wide, two to three times as large as round outer tubercle; plantar surface lacking supernumerary tubercles; toes lacking lateral fringes and basal webbing; subarticular tubercles large, round, simple, non-conical; tips of toes rounded, not dilated; hindlimbs short, shank 34.2–35.7 ($\bar{x}$ = 35.2) % SVL.

In preservative, the dorsal surfaces are brown with indistinct

darker brown mottling; no color pattern is evident. *P. brunneus* lacks distinct canthal and supratympanic stripes, labial bars, and an anal triangle. The ventral surfaces are paler than the dorsum and vary from dusky gray to brown. One individual (USNM 192909) has narrow dark brown bars on the shank and tarsus.

Measurements of the holotype in mm.—SVL 25.8, shank 9.1, head width 9.7, head length 8.8, eyelid width 1.8, IOD 2.1, tympanum 1.3, eye length 2.7, eye–nostril 1.8.

Etymology.—Latin, in reference to the drab coloration of browns and grays.

Natural history.—The four specimens were collected by day beneath logs in a wet pasture at 3150 m on the high Amazonian slopes of the eastern Andean cordillera. The female (USNM 192910) contains large (3.5 mm in diameter), yellow, ovarian eggs and has convoluted oviducts. The testes of the males are not especially large or swollen and are not black (in contrast to the black testes in male *E. curtipes* collected syntopically).

Distribution.—Known only from the type-locality (Fig. 14).

Phrynopus cophites new species

Fig. 15

Holotype.—KU 138884, adult female, S slope Abra Acanacu, 14 km NNE Paucartambo, Depto. Cuzco, Perú, 3400 m, collected 13 January 1971 by Thomas H. Fritts.

Paratypes.—(30) KU 138885–908, 138911–16, N slope Abra Acanacu, 27 km NNE Paucartambo, Depto. Cuzco, Perú, 3400 m.

Diagnosis.—A small *Phrynopus* (♂♂ 18.0–22.7 mm, ♀♀ 21.9–29.3 mm SVL); skin of dorsum and venter coarsely areolate; first finger shorter than second; tips of digits lacking apical swelling; toes lacking lateral fringes and basal web; two metatarsal tubercles, inner slightly larger than or equal to outer; no tarsal tubercle or fold; tympanum, columella, and cavum tympanum absent; snout rounded in lateral profile; males lacking vocal sac and slits; prevomerine teeth and dentigerous processes lacking, dentigerous ramus of prevomer present; frontoparietals not bearing crests, frontoparietal fontanelle present; nasals separated medially, small; anterior ramus of parasphenoid not reaching palatines; dorsum gray to brown with or without diffuse mottling; venter brown with brown mottling; throat usually more pale than venter.

Description.—Head narrower than body (Fig. 15), head wider than long; head width 31.1–36.1 ($\bar{x}$ = 33.7) % SVL; snout round in dorsal view, round to truncate in lateral profile, tip of snout level with edge of lip; canthus rostralis moderately sharp, concave; loreal region flat, sloping to lip; lips not flared; nostrils weakly protuberant, directed anterolaterally; snout very short, E–N much less than eye length; interorbital region flat; upper eyelid width 66.6–86.7 ($\bar{x}$ = 76.2) % IOD; temporal region swollen (parotoid gland-like); no supratympanic fold; tympanic annulus, columella, and cavum tympanicum absent; postrictal tubercles present, not prominent; choanae small, round, situated well anteriad on palate, not concealed by palatal shelf of maxillae when roof of mouth is viewed from di-

rectly above; prevomerine teeth and dentigerous processes absent; tongue slightly longer than wide, not notched posteriorly, posterior one–fifth to one–fourth free; males lack vocal slits and vocal sac.

Skin of dorsum finely areolate, areolation increasing in size and prominence posteriorly and on flanks; skin of venter (including throat) coarsely areolate; no discoidal folds; tubercles on dorsum sometimes coalesce forming short, irregular vertebral, paravertebral, and dorsolateral folds or ridges; dorsolateral ridges most prominent anteriorly; no ulnar tubercles or ridge; palmar tubercle not bifid, as large as thenar tubercle (Fig. 7); a third, outer, palmar tubercle occasionally present, but difficult to discern from low supernumerary tubercles on palm; subarticular tubercles low, flat, round, simple; fingers lacking lateral fringes; tips of fingers usually lacking apical swelling; first finger shorter than second; base of thumb swollen in reproductively active males.

Heel bearing several small tubercles; tarsus areolate and lacking distinct tubercles or folds on inner and outer edges; two metatarsal tubercles, inner slightly larger than outer, both longer than wide (Fig. 8); plantar surface areolate; subarticular tubercles low, round, simple, more prominent than those of fingers; toes lacking lateral fringes and basal webs; tips of toes narrow, little or no apical bulbing; hindlimbs very short, heel of adpressed limb not reaching forearm insertion in adults, but reaching axilla in juveniles; shank 29.2–33.8 ($\bar{x} = 31.7$) % SVL in ♂♂, 31.9–35.7 ($\bar{x} = 33.9$) in ♀♀.

In preservative, the ground color is gray to dull brown with or without brown to black mottling. The venter is gray to dark brown with mottling of a darker brown. The throat is usually paler than the venter. A few individuals have a thin sagittal and transverse pectoral line on the venter and throat. The flanks are darker than the dorsum; some individuals have faint, thin, cream–colored bars on the flanks. The darker specimens have canthal stripes and labial bars. The limbs are not barred and the posterior surfaces of the thighs are gray to dark brown.

In life, *P. cophites* is dull brown to pale tan above or has a mottled pattern of olive–brown and black to brown and greenish–yellow or red. The venter is dull gray. Males have an orange cast to the throat.

Measurements of the holotype in mm.—SVL 29.3, shank 9.2, head width 10.1, eyelid width 2.2, interorbital distance 2.8. The holotype is a gravid female with convoluted oviducts and large yellow eggs (2.0–2.5 mm in diameter).

Etymology.—From Greek, *kophos*, meaning deaf; in reference to the absence of an external and middle ear.

Natural history.—Phrynopus cophites was found in paramo and elfin forest habitats in a ravine on the Cadena de Paucartambo at elevations of 3400 to 3450 m. The majority of the specimens were collected syntopically with *P. peruvianus*. As in *P. peruvianus*, the

females of *P. cophites* are gravid. Males of *P. cophites* lack vocal and auditory apparatus, and presumably do not call.

Distribution.—Known from both the north and south slopes of the Abra Acanacu, a pass in the Cadena de Paucartambo, on the northwestern end of the Cordillera Carabaya, in Departamento Cuzco, Perú, between 3400 and 3450 m (Fig. 14).

Remarks.—Earlessness and the very short limbs readily distinguish *P. cophites* from all other known species of *Phrynopus. P cophites* has a short first finger, areolate skin, and lacks prevomerine teeth as in *P. montium, P. simonsii,* and *P. wettsteini. P. montium* and *P. wettsteini* have complete ears concealed beneath the skin and longer legs than *P. cophites. P. nanus, P. simonsii,* and *P. cophites* are the only earless species of the genus, but differ in several respects. *P. cophites* has a frontoparietal fontanelle, small nasals, small prevomers, and short rami of the parasphenoid. Judging from dissections, the skull of *P. simonsii* is similar to that of *P. parkeri;* an idea of the differences between *P. cophites* and *P. simonsii* can be obtained by comparing the skull of *P. parkeri* with that of *P. cophites* (Figs. 10, 12). If the similarities of the skulls are a useful index of relationship, *P. cophites* is allied to *P. laplacai, P. montium, P. peruanus,* and *P. wettsteini,* and less closely to *P. peruvianus,* with little relationship to the northern *Phrynopus* (*brunneus, flavomaculatus, parkeri, peraccai, pereger,* and *simonsii*).

Phrynopus flavomaculatus (Parker), new combination

Eleutherodactylus flavomaculatus Parker, 1938:440 (*Holotype.*—BMNH 1935. 11.3.16/1947.2.16.11, 15 km E Loja, Prov. Loja, Ecuador, 3000 m).
Niceforonia flavomaculata—Lynch, 1969:273.

Diagnosis.—A large *Phrynopus* (♂♂ 26.0–32.5 mm, ♀♀ 29.2–42.6 mm SVL); skin of dorsum and venter smooth; first finger longer than second; tips of digits not bulbous; toes lacking basal webbing and lateral fringes; two metatarsal tubercles, equal in size; tarsus lacking tubercles or folds; tympanum visible, 37.8–51.4 % eye length; snout sloping in lateral profile; male with vocal slits and subgular vocal sac; prevomerine teeth present on prominent processes lying median and posterior to choanae; frontoparietals complete, bearing prominent lateral crests (Fig. 9); nasals large, in broad median contact; anterior ramus of parasphenoid long, contacting palatines; median ramus of pterygoid in contact with parasphenoid alae; dorsum brown with darker brown blotches, venter brown with large yellow spots, throat dark brown.

Description.—See Parker (1938).

Natural history.—*P. flavomaculatus* is usually found beneath rocks or logs in paramo and subparamo habitats. At a locality north of San Lucas (Loja Prov), I found *P. flavomaculatus* in the more xeric sites within the subparamo and found *Telmatobius niger* beneath logs in the wet cienegas of the paramo. A single egg mass (KU 121354) was collected in June 1968 beneath a log with a female *P. flavomaculatus.* The egg mass and adult frog were about 1 m apart.

Distribution.—Known from between 2215 and 3100 m on the eastern Andean Cordillera in southern Ecuador (Fig. 14).

Phrynopus laplacai (Cei), new combination

Syrrhophus laplacai Cei, 1968:139 (*Holotype.*—IBN/UNC 1251–1, 3 km W Pongo on road to Coroico from La Paz, Depto. LaPaz, Bolivia, 3400 m).
Niceforonia laplacai—Lynch, 1969:273.

Diagnosis.—A moderate sized *Phrynopus* (♂♂ 27–31 mm, ♀♀ 28–33 mm SVL); skin of dorsum and venter areolate; first finger longer than second; tips of digits bulbous; toes lacking basal webbing and lateral fringes; two metatarsal tubercles, inner slightly larger than outer; no tarsal fold or tubercle; tympanum concealed beneath skin; snout truncate in lateral profile; males with vocal sac and vocal slits; prevomerine teeth and dentigerous processes lacking; frontoparietals complete, lacking crests; nasal bones narrowly separated; anterior ramus of parasphenoid not reaching palatines; dorsum brown, mottled with cream; venter cream with brown flecking, throat black in males.

Description.—See Cei (1968).

Distribution.—Known only from the vicinity of the type-locality (Fig. 14).

Remarks.—*P. laplacai, P. montium,* and *P. wettsteini* form a group of closely allied southern species. Males of *laplacai* and *wettsteini* are easily recognized by the black throats; females of *wettsteini* also have black throats. Too few specimens are available of the three taxa to permit a definitive assessment of the distinctions presently understood. The greatest similarities are between *laplacai* and *wettsteini.* The differences cited in the diagnoses may well reflect the small sample sizes, age in perservative, or method of preservation. If the type-locality for *wettsteini* (see species account) is actually in northern Peru, then it seems very unlikely that the two names apply to the same population—the specimens on which they are based were collected at localities more than 1600 kilometers (airline) apart, and at altitudes of 2000 and 3400 meters. In view of the uncertainty concerning the type-locality of *wettsteini* this argument is moot. Cei (1968) only compared *laplacai* to *montium*—these two names are certainly not synonymous.

Phrynopus montium (Shreve), new combination

Syrrhopus montium Shreve, 1938:406. (*Holotype.*—MCZ 22858, Cascas, near Huashuasi, Depto. Junín, Perú).
Syrrhophus montium—Gorham, 1966:166.
Niceforonia montia—Lynch, 1968:291.

Diagnosis.—A moderate-sized *Phrynopus* (21–29 mm SVL); skin of dorsum and venter areolate; first finger shorter than second; tips of digits weakly bulbous; toes lacking basal webbing and lateral fringes; two metatarsal tubercles, inner much larger than outer; tarsus lacking tubercles or folds; tympanum concealed beneath skin; snout rounded in lateral profile; males with vocal sac and slits; prevomerine teeth and dentigerous processes absent, dentigerous ramus of prevomer present; frontoparietals complete, lacking crests; nasals widely separated; anterior ramus of parasphenoid short, not reaching

palatines; median ramus of pterygoid narrowly separated from parasphenoid ala; dorsum dark brown, venter cream suffused with brown; throat not conspicuously darker than venter.

Distribution.—Known only from the type-locality (Fig. 14).

Remarks.—The data available for *P. montium* are too scanty, as for *P. laplacai* and *P. wettsteini*, to comment beyond that given in the remarks for those two species.

Phrynopus nanus (Goin and Cochran), new combination

Niceforonia nana Goin and Cochran, 1963:499 (*Holotype.*—USNM 150643, Paramo de la Rusia, Depto. Santander, Colombia).

Diagnosis.—A small *Phrynopus* (female holotype 20.5 mm SVL); skin of dorsum granular, that of venter coarsely areolate; first finger shorter than second; fingers and toes not dilated at tips; toes bearing lateral fringes and basal webbing; two metatarsal tubercles, inner slightly larger than outer; tarsus lacking distinct tubercles or folds; tympanum absent (or greatly reduced in size); snout rounded in lateral profile; prevomerine teeth present on small dentigerous processes; frontoparietals not bearing crests, complete; nasals large, in contact; body brown without distinct pattern, venter paler than dorsum.

Description.—Goin and Cochran (1963); Cochran and Goin (1970).

Distribution.—Known only from the type-locality.

Remarks.—With only the holotype available, few additional anatomical features can be noted for this species. Goin and Cochran (1963) described the skin of the venter as coarsely areolate, but at present (1973) the skin of the venter appears smooth except posteriorly where very coarse granulations are evident. I suspect that the entire venter of the specimen was once areolate and that the now smooth appearance of most of the venter is an artifact of preservation.

The most perplexing problem involving this species is its relationships to the other species here called *Phrynopus*. Comparisons of the character mosaics of the other species of simple-toed eleutherodactylines with that of *P. nanus* prompts the conclusion that *nanus* is most similar to *simonsii*. The similarity may be in part spurious in that the character mosaics for each species are incomplete. The two species are readily distinguished in that *simonsii* lacks prevomerine dentigerous processes, has glandular dorsolateral folds, is considerably larger, and has vertical bars on the lower flanks.

The resemblance of *P. nanus* to the other northern *Phrynopus* is limited to the sharing of prevomerine dentigerous processes. The Ecuadorian species of the genus uniformly have smooth skin on the venter, the first finger longer than the second, and well-developed ears. *P. nanus* may prove to be an independent offshoot of *Eleutherodactylus*, convergent with *Phrynopus* in digit structure. This question cannot be answered until more material is available.

Phrynopus parkeri new species

Fig. 16

Holotype.—KU 135278, an adult male from the summit of the cordillera between Chanchaque and Huancabamba, Depto. Piura, Perú, 3100 m, collected 11 May 1970 by Thomas H. and Patricia R. Fritts.

Paratypes.—(32) KU 135279–305, 135307–11, collected syntopically with the holotype.

Diagnosis.—A moderate–sized *Phrynopus* (♂♂ 21.4–24.2 mm, ♀♀ 27.4–35.0 mm SVL); skin of dorsum and venter smooth; first finger longer than second; digit tips weakly bulbous; toes lacking lateral fringes and basal webbing; two metatarsal tubercles, inner twice size of outer to equal in size to outer; tarsus lacking distinct tubercles or folds; tympanum present, concealed beneath skin; snout sloping in lateral profile; prevomerine teeth present on well-developed processes medial and posterior to choanae; frontoparietals complete, lacking crests; nasals large, in median contact; anterior ramus of parasphenoid long, in contact with palatines; median ramus of pterygoids in contact with parasphenoid alae; dorsum brown with darker mottling, venter cream with brown reticulations, throat darker than venter.

Description.—(Fig. 16.) Head narrower than body, head as wide as long or slightly wider than long in males, wider than long in females, head width 34.3–40.0 ($\bar{x}$ = 36.6) % SVL; snout rounded in dorsal view, sloping in lateral profile (Fig. 4); canthus rostralis sharp, concave; loreal region concave; lips not flared; nostrils lateral, weakly protuberant; snout short, eye length slightly greater than E–N; interorbital region flat, no cranial crests; upper eyelid width 84.1–110.0 ($\bar{x}$ = 93.3) % IOD in males, 68.9–95.6 ($\bar{x}$ = 81.3) % in females; tympanum concealed beneath skin; supratympanic fold poorly–defined; tongue large, oval, not notched posteriorly, posterior one–fifth free; choanae small, round, not concealed by palatal shelf of maxillae; prevomerine dentigerous processes present, each 6 to 8 times size of a choana, processes slanted posteriorly, wider than long, each bearing 3–6 teeth, processes separated by distance equal to width of a choana; male with vocal slits and subgular vocal sac.

Skin of body smooth except on posteroventral surfaces of thighs; discoidal folds prominent posteriorly; no dorsolateral folds; forearm lacking ulnar tubercles or folds; three palmar tubercles, outer minute (Fig. 6); thenar surface bearing a few ill-defined supernumerary tubercles, subarticular tubercles of fingers low, round, simple; fingers not fringed, tips round and weakly bulbous; first finger longer than second (Fig. 6).

Tarsus and heel lacking tubercles or folds (except in some females where an idefinite inner tarsal tubercle is evident); two metatarsal tubercles, neither enlarged nor compressed, inner oval, relative sizes of tubercles, varies from equal in size (most individuals) to inner twice size of outer; plantar surface bearing a few indefinite supernumerary tubercles; subarticular tubercles of toes flat, round, simple, same size as those of fingers; toes lacking lateral

fringes and basal webbing; tips of toes simple and weakly bulbous; hindlimbs short, heel of adpressed limb reaches to base of forearm and tympanic area; shank 37.1–43.8 ($\bar{x} = 40.1$) % SVL.

In preservative, the dorsal surfaces are gray–brown to reddish–brown with or without a hairline cream sagittal stripe. Some individuals have a broad dorsal band of dusky cream or dull brown and a few individuals have indefinite dorsolateral stripes. The flanks are darker than the dorsum and have a nebulose pattern of browns. The lips are not marked except for an indefinite cream stripe in some specimens. The limbs are not barred in most specimens; some individuals do have faint barring on the shanks. The posterior surfaces of the thighs are unicolor brown or brown with small cream flecks. The venter is cream or cream mottled with brown; in some specimens the marbling is so intense that the venter and the undersides of the thighs are pale to dark brown. The specimens with the cream sagittal line have another line along the posterior surface of the thigh, underside of the shank, inside of the tarsus continuing onto the plantar surface, and on the ulnar region continuing onto the thenar surface.

In life, *P. parkeri* has a ground color of olive–brown, gray–brown, reddish–brown, dark–brown, or metallic green–brown. The flanks are dark–brown to gray–brown flecked with metallic green. The posterior surfaces of the thighs are dark-brown or black with yellow spots and blotches. The ventral surfaces are charcoal–gray or black with large egg–yolk yellow blotches in males. The venter of females tends to be unicolor egg–yolk yellow with indefinite brown reticulations. Males have gray throats whereas females have a yellow–green haze on the throat. The face is marked with an indefinite dark–brown canthal stripe and in some individuals with a beige–white labial stripe. The iris is dark-brown (T. H. Fritts field notes, 11 May 1970).

Measurements of the holotype in mm.—SVL 22.6, shank 9.2, head width 8.1, head length 8.1, eyelid width 2.2, IOD 2.5.

Etymology.—Named for Hampton W. Parker, the first author to deal with the complex of frogs here called *Phrynopus.*

Natural history.—All of the known specimens were collected by day beneath rocks along the road between Chanchaque and Huancabamba, Piura, Perú, at 3100 m. The west slope of the cordillera is dry and chaparrel–like, whereas the east slope and summit of the cordillera supports a moist, elfin forest with shrubs and shrub–like bushes 2–3 m high. No reproductive activity was noted by the collectors although the females in the type–series have mature ovarian eggs.

Distribution.—Known only from the type–locality (Fig. 14).

Remarks.—*P. parkeri* is most closely related to *P. flavomaculatus* and *P. pereger.* The similarity between the three species is evident in all characteristics cited and the three differ only in *flavomaculatus*

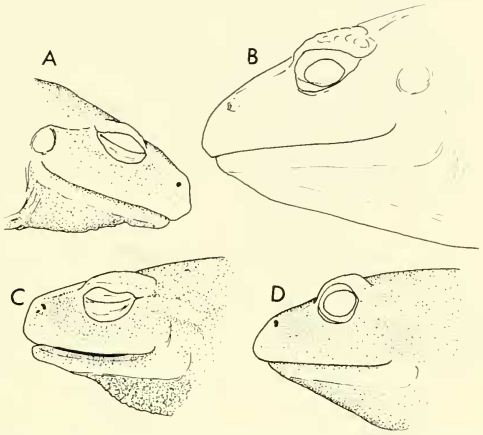

FIG. 4.—Lateral views of heads of (A) *Phrynopus brunneus*, USNM 192909, (B) *P. flavomaculatus*, KU 142199, (C) *P. simonsii*, BMNH 1947.2.15.43, and (D) *P. parkeri*, KU 135298.

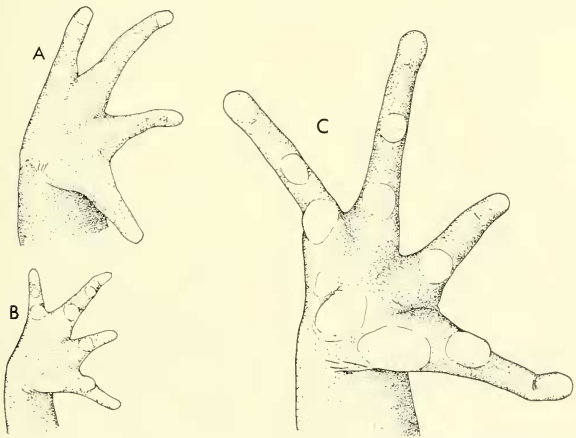

FIG. 5.—Palmar views of hands of (A) *Phrynopus brunneus*, USNM 192911, (B) *P. peraccai*, KU 117795, and (C) *P. flavomaculatus*, KU 119722.

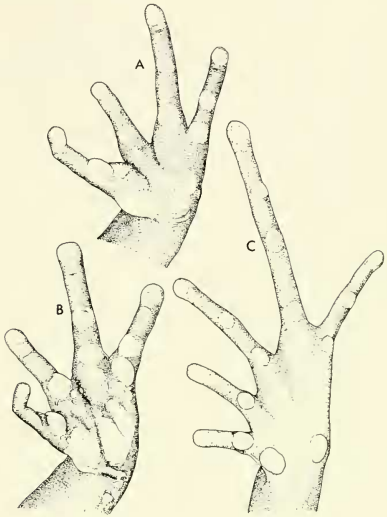

FIG. 6.—Palmar views of hands of (A) *Phrynopus parkeri,* KU 135282, (B) *P. simonsii,* BMNH 1947.2.15.43, and plantar view of foot of (C) *P. parkeri,* KU 135298.

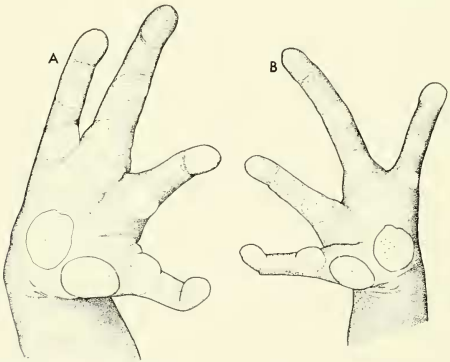

FIG. 7.—Palmar views of hands of (A) *Phrynopus cophites,* KU 138884, and (B) *P. peruvianus,* KU 138138.

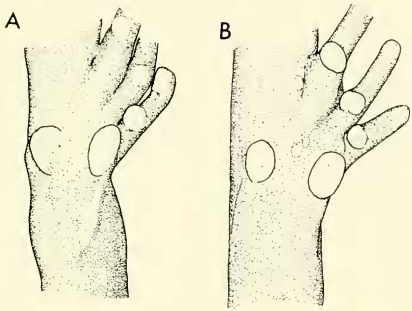

FIG. 8.—Distal tarsus and proximal portion of foot (plantar views) of (A) *Phrynopus peruvianus*, KU 138138, and (B) *P. cophites*, KU 138911.

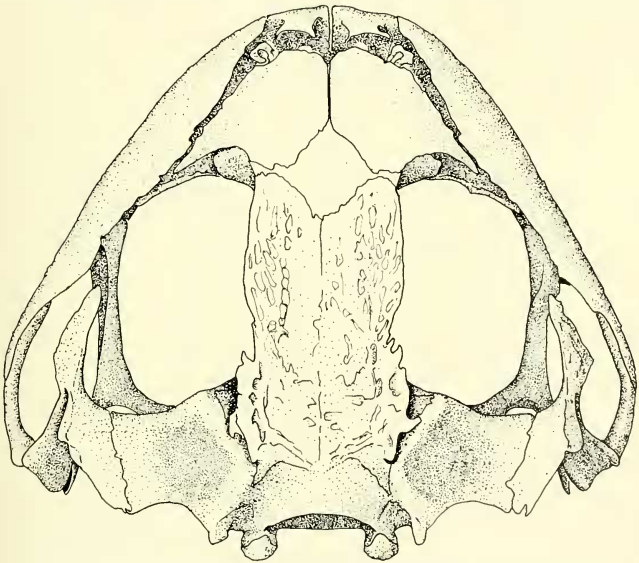

FIG. 9.—Skull of *Phrynopus flavomaculatus* in dorsal view (KU 119743).

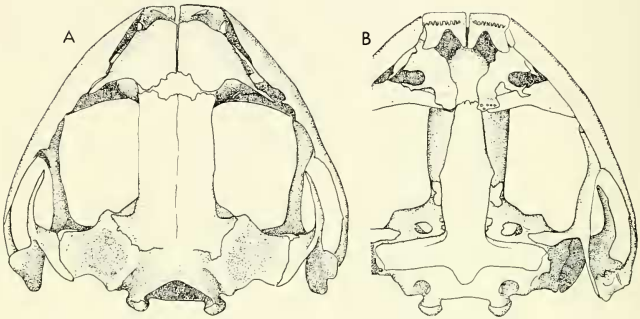

FIG. 10.—Skull of *Phrynopus parkeri* (KU 135306) in dorsal (A) and ventral (B) views.

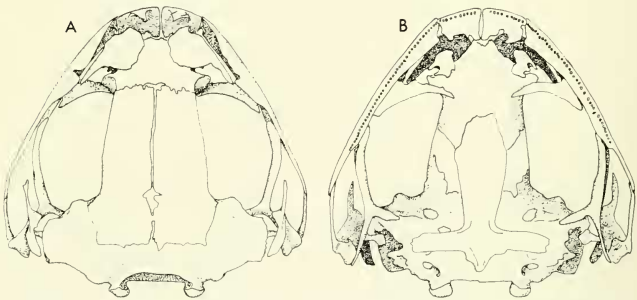

FIG. 11.—Skull of *Phrynopus peruvianus* (KU 138926) in dorsal (A) and ventral (B) views.

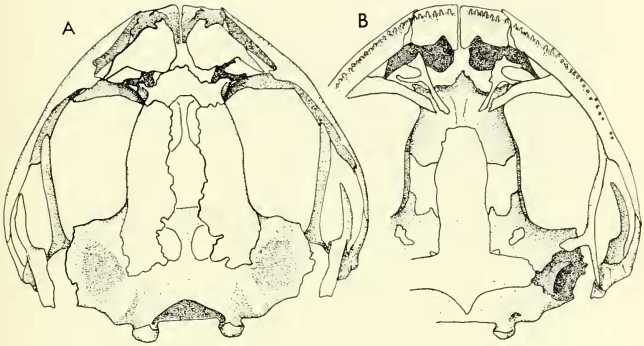

FIG. 12.—Skull of *Phrynopus cophites* (KU 138909) in dorsal (A) and ventral (B) views.

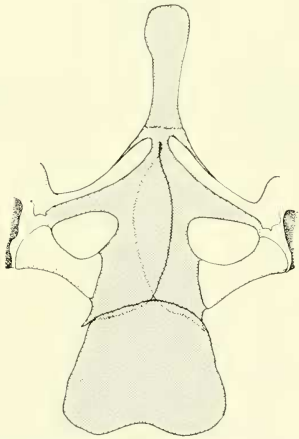

FIG. 13.—Ventral view of pectoral girdle of *Phrynopus peruanus* (UMMZ 89477).

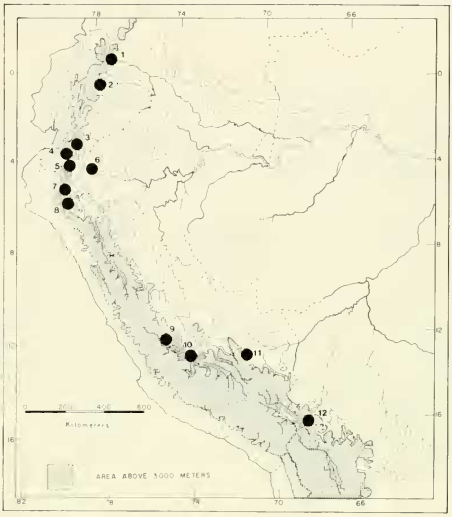

FIG. 14.—Distribution of *Phrynopus* in Bolivia, Ecuador, and Perú. *P. brunneus* (1), *P. cophites* (11), *P. flavomaculatus* (3-5), *P. laplacai* (12), *P. montium* and *P. peruanus* (9), *P. parkeri* (7), *P. peraccai* (2), *P. pereger* (10), *P. peruvianus* (11), *P. simonsii* (8), and *wettsteini* (6).

FIG. 15.—Dorsal and ventral views of *Phrynopus cophites* (KU 138895, 25.4 mm SVL).

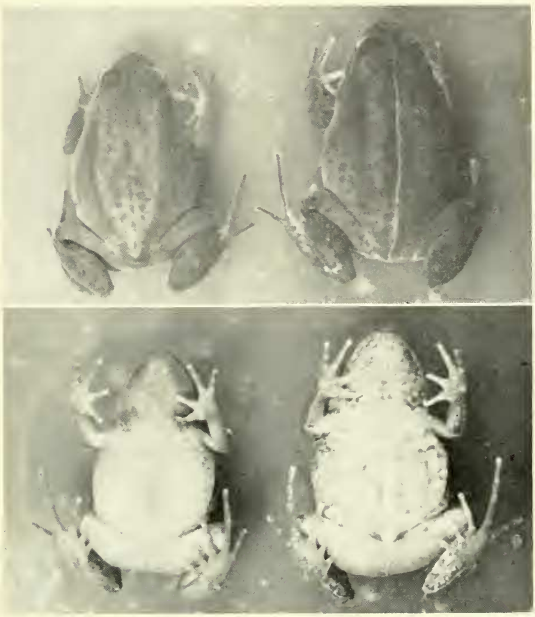

FIG. 16.—Dorsal and ventral views of *Phrynopus parkeri* (left, KU 135297, 31.3 mm SVL; right, KU 135298, 35.0 mm SVL).

FIG. 17.—*Phrynopus peruvianus* (left, KU 138950, 25.1 mm SVL; middle and right, KU 138940, 20.2 mm SVL).

having prominent cranial crests and reaching a larger size, and in *parkeri* having the tympanic annulus concealed beneath the skin.

Phrynopus peraccai new species

Niceforonia festae—Lynch, 1968:289–93; 1969:273; 1970:139; 1971:157.

Holotype.—USNM 160947, an adult female collected 1 km W Papallacta, Napo Prov., Ecuador, 3155 m, 6 July 1962 by James A. Peters, P. Spoecker, and M. Olalla.

Paratypes.—(16) ECUADOR, *Napo Prov.:* Papallacta, 3110 m, USNM 164397, MIZ 820; 1 km W Papallacta, 3155 m, KU 111430, USNM 160955–59, 160961, 160966–68, 164398; 4 km W Papallacta, 3300 m, KU 117795–96; Laguna Papallacta, 3350 m, KU 109171.

Diagnosis.—A small *Phrynopus* (adult ♀♀ 19.0–21.6 mm SVL); skin of dorsum smooth with flat warts on eyelids and flanks, that of venter smooth; first finger longer than second; tips of digits not bulbous; toes lacking lateral fringes and basal webbing; two metatarsal tubercles, equal in size or outer larger; tarsus lacking tubercles or folds; tympanum visible externally, not prominent, its length 1/3–2/5 that of eye; snout rounded to truncate in lateral profile; males not known; prevomerine dentigerous processes prominent, bearing teeth; frontoparietals complete, lacking crests; nasals separated, moderately large; anterior ramus of parasphenoid long but not reaching palatines; median ramus of pterygoid in contact with parasphenoid alae; coloration brown, dorsum darker than venter and bearing indefinite blotches.

Description.—Head narrower than body, head wider than long; head width 35.0–40.7 ($\bar{x} = 37.5$) % SVL; snout round in dorsal view, rounded to truncate in lateral profile; snout short, E–N 60.0–100.0 ($\bar{x} = 77.4$) % eye length; canthus rostralis moderately sharp, concave; loreal region weakly concave, sloping gradually to non-flared lips; nostrils directed dorsolaterally, weakly protuberant; interorbital space flat, no cranial crests; upper eyelid width 63.4–90.9 ($\bar{x} = 75.1$) % IOD; supratympanic fold indistinct, obscuring upper edge of tympanum; tympanum visible externally, not prominent, higher than long, separated from eye by 1½ times tympanum width; tympanum length 35.1–51.3 ($\bar{x} = 41.8$) % eye length; males not known; tongue about as long as wide, not notched posteriorly, posterior one-fourth to one-third not adherent to floor of mouth; choanae small, round, not concealed by palatal shelf of maxillae; prevomerine dentigerous processes present, bearing 0–7 ($\bar{x} = 4.4$) teeth/process, wider than long, median and posterior to choanae, separated medially by distance equal to width of a choana, teeth in a transverse row; prevomerine dentigerous process 3–4 times width of a choana.

Skin of dorsum smooth except for low, obscure warts on eyelids and sometimes flanks, skin of venter smooth; no dorsolateral folds; discoidal folds obscure; forearm lacking ulnar tubercles or folds; palmar tubercle bifid, as large as thenar tubercle (Fig. 5); thenar surface lacking supernumerary tubercles; subarticular tubercles round, non-conical, simple; fingers not fringed; first finger longer than second; tips of digits pointed, not bulbous.

Heel and tarsus lacking tubercles and folds; two metatarsal

tubercles, inner longer than wide, outer about as long as wide; metatarsal tubercles equal in size or outer larger than inner; no supernumerary plantar tubercles; subarticular tubercles not distinct, round, simple, smaller than those of fingers; toes lacking lateral fringes and basal webbing; tips of toes rounded, not bulbous; hindlimbs short, shank 33.7–40.4 ($\bar{x} = 37.0$) % SVL.

In preservative, *P. peraccai* is brown. The dorsum is darker than the venter. The limbs are faintly barred and the dorsum bears indistinct darker brown markings (interorbital bar, scapular and sacral chevron, anal triangle). Labial bars are weakly evident and a dark supratympanic stripe is present bordered below by a cream postrictal stripe. The venter is finely punctated with cream.

In life, *P. peraccai* is gray–brown with darker brown markings on the dorsum and cream spots on the venter.

Measurements of the holotype in mm.—SVL 21.7, shank 7.6, head width 8.0, head length 6.9, eyelid width 1.7, IOD 2.1, tympanum length 0.9, eye length 2.4, eye–nostril 1.8. The holotype has 4 and 5 prevomerine teeth on the right and left processes respectively, and is a gravid female with heavily convoluted oviducts and large yellow eggs (2.5–3.0 mm in diameter).

Etymology.—Named for Mario G. Peracca.

Natural history.—I have examined 21 specimens of this species, all of which were collected within 5 km of Papallacta, Ecuador. All of the specimens are females. The four smallest individuals (USNM 160958, 160966–68) are 16.1–18.3 mm SVL and have weakly convoluted oviducts and small ovarian eggs (less than 1.0 mm in diameter). The next smallest individual (KU 117796, 19.0 mm SVL) contained large eggs (2.0–3.0 mm in diameter) and has weakly convoluted oviducts. Individuals more than 20.0 mm SVL have large eggs and heavily convoluted oviducts. Gravid females have been collected in March, July, and November but no egg clutches have been found. All specimens were collected beneath rocks in the grassy paramo or subparamo habitats that surround Papallacta.

Distribution.—Known only from the vicinity of Papallacta, Napo Prov., Ecuador, between 3000 and 3350 m (Fig. 14).

Remarks.—Since 1968 this species has been called *Niceforonia festae* (Peracca). I have now examined 12 syntypes of *festae* BMNH 1926.12.4.1/1947.2.15.47, MIZ 428(9), 819 (lectoholotype of *Paludicola festae,* here designated), 820. Eleven of the specimens are the frog I (1968) named *Eleutherodactylus trepidotus.* The other specimen is a *Phrynopus peraccai.* The description of *Paludicola festae* clearly applies to the species with narrow, but complex, digits (*E. trepidotus*) and cannot be applied to the simple–toed species (*P. peraccai*).

Paludicola festae Peracca is the oldest name for *Eleutherodactylus trepidotus* Lynch, but is not available because in the same paper naming *Paludicola festae,* Peracca (1904) named *Hylodes*

festae, identical with *Eleutherodactylus galdi* (Lynch, 1974). *Paludicola festae* Peracca is thus a secondary homonym, and the correct name for the narrow-toed *Eleutherodactylus* at Papallacta is *E. trepidotus* Lynch.

I have previously (1970) mentioned that three species of eleutherodactyline frogs found in the vicinity of Papallacta were known only from females. In spite of large samples, several different collectors with presumably different techniques, and collections at different times of the year, I had not found male *E. trepidotus* and had begun to consider it all female. However, two of the specimens in the syntypic series of *Paludicola festae* are males (vocal sac and slits, testes). The sex ratio remains impressively biased (2 males: 81 females) for this species. In light of this sex ratio, the absence of males in a sample of only 21 *Phrynopus peraccai* takes on less significance and may simply reflect secretiveness of the males.

A close relationship between *P. brunneus, P. flavomaculatus, P. parkeri, P. peraccai* and *P. pereger* is suggested by the commonality of smooth skin of the venter, first finger longer than the second, and prominent prevomerine dentigerous processes. The sloping snouts of *P. flavomaculatus* and *P. parkeri* are distinctively different from the truncate or rounded snouts seen in *P. brunneus* and *P. peraccai.* Little osteological data are available for *P. brunneus,* but what is available suggests that *P. brunneus* is intermediate between *P. peraccai* and the sloping-snout species. *P. brunneus* is probably the closest ally of *P. peraccai.* The two species differ in size (*peraccai* is smaller), relative sizes of the metatarsal tubercles (inner much larger than the outer in *brunneus*), and head shape (subjective) in addition to the meager osteological differences gleaned by dissection of one specimen of *brunneus* and three cleared and stained skeletons of *peraccai.*

Phrynopus pereger new species

Holotype.—LSUMZ 26101, adult female, part of a series taken between Mitupucuru and Yuraccyacu, Depto. Ayacucho, Perú, by Richard Thomas, 11–13 May 1971.

Paratypes.—LSUMZ 26102–10, KU 151908–09, topotypes; LSUMZ 26117–23, 26255, Yuraccyacu, on Tambo–Valle del Apurimac trail, 2650 m; LSUMZ 26124–31, Ccarapa, below Tambo on Ayacucho–Valle del Apurímac trail, 2460 m, Depto. Ayacucho, Perú.

Diagnosis.—A moderate-sized *Phrynopus* (♂♂ 20.5–25.4, ♀♀ 24.2–31.8 mm SVL); skin of dorsum and venter smooth; first finger longer than second; digit tips bulbous; toes lacking lateral fringes and basal webbing; two metatarsal tubercles, inner slightly larger than outer; tarsus lacking tubercles or folds; tympanum visible, not prominent, its length 31.2–50.0 % eye length; snout rounded in lateral profile; prevomerine teeth present on well-developed processes posteromedial to choanae; frontoparietals complete, lacking prominent crests; nasals large, in median contact; anterior ramus of parasphenoid in tenuous contact with palatines; median pterygoid ramus in contact with parasphenoid alae; brown above with diffuse dark blotches, usually with a

pale interorbital bar, limbs not barred, venter brown with indefinite pale brown spots to cream with brown suffusion or indefinite brown spots.

Description.—Head narrower than body, broader than long except in juveniles; head width 35.8–40.8 ($\bar{x}$ = 37.4) % SVL; snout subacuminate in dorsal view, rounded in lateral profile; snout short, E–N slightly less than eye length; canthus rostralis sharp, concave; nostrils weakly protuberant, directed dorsolaterally; loreal region concave, sloping abruptly to non-flared lips; interorbital space flat (no cranial crests), broad; upper eyelid width 74.1–95.8 ($\bar{x}$ = 87.5) % IOD; upper eyelid bearing one or two tubercles and/or ridges running posteromedially onto occiput; supratympanic fold obsolete, covering upper edge of ear; ear visible, higher than long, its length 38.6–50.0 ($\bar{x}$ = 43.4) % eye length in males, 31.2–45.4 ($\bar{x}$ = 39.4) % in females; choanae moderate-sized, wider than long, about size of a prevomerine dentigerous process, well within maxillary arch; prevomerine dentigerous processes posteromedial to choanae, round, each bearing 3–6 teeth; tongue longer than wide, not notched posteriorly, posterior one-third not adherent to floor of mouth; males with vocal slits, subgular vocal sac.

Skin of dorsum finely shagreened, some specimens with thin sagittal and dorsolateral ridges; skin of venter smooth, that below and lateral to vent coarsely areolate; no discoidal folds; no ulnar tubercles or folds; palmar tubercle bifid and larger than thenar tubercle; subarticular tubercles round, flat; fingers lacking lateral fringes; digits with moderate apical swelling, no discs; first finger longer than second.

Shank 39.0–48.6 ($\bar{x}$ = 43.6) % SVL; no tarsal or heel tubercles; two prominent metatarsal tubercles, inner longer than wide, 1½ times size of outer (also longer than wide); no supernumerary plantar tubercles; subarticular tubercles round or slightly longer than wide, less flattened than those of fingers; toes lacking lateral fringes and basal webbing; digit tips swollen; lacking discs.

In preservative, *P. pereger* is medium to dark brown above with diffuse darker blotches; the limbs are not or only weakly barred; canthal and supratympanic stripes are dark brown, the latter edged below by a cream postrictal stripe; lips not or only weakly barred; flanks paler than dorsum and occasionally appearing reticulated, especially in groin; a large dark brown spot or bar is present on the proximal surface of the anterior face of the upper arm; anterior and posterior surface of thighs dark brown without spots but some individuals have cream spots on the posterior surface of the thighs; black or dark brown anal patch present, marked in some specimens by cream lines extending along the posterior surface of the thighs; in most specimens the venter is uniform brown with indefinite paler brown areas; in some specimens the venter is largely cream with a suffusion of brown or indefinite brown spots; the extreme ventral coloration is cream densely marbled with brown. The throat tends

to be darker than the rest of the venter. Most specimens have a pale interorbital bar or spot.

In life, *P. pereger* has a dark gray, reddish-brown, or dark gray-brown ground color with little indication of pattern. The flanks are yellowish brown to dull yellow with an orange suffusion ventrally. The venter varied from brown with orange spots to off-white with black to gray spotting and/or suffusion. If pale canthal lines were present, they were pale yellow. (R. Thomas field notes.)

Measurements of holotype in mm.—SVL 28.8, shank 12.9, head width 10.7, head length 10.7, eyelid width 2.4, IOD 2.6, tympanum length 1.2, eye length 3.0, eye-nostril 3.0.

Etymology.—Latin, *pereger,* on a journey, in reference to the wide geographic hiatus between *P. pereger* and the other members of the predominantly northern *flavomaculatus* group.

Natural history.—All of the specimens of *P. pereger* were collected by day in terrestrial situations (beneath rocks, in leaf litter, and in moss along a road cut). All of the localities at which the frogs were found are described by the collector as dwarf cloud forest (*monte chico* of Terborgh, 1971), characterized by the small, microphyllous trees.

A total of six males (2 immature, no vocal slits) and 23 females (4 immature, straight oviducts) comprise the total sample of this species. The 19 adult females contain large, yellow eggs. In two females, the largest eggs are only 1.5–1.7 mm in diameter contrasting strongly with the much larger eggs (2.6–4.0 mm) in the other females.

The cleared and stained females (KU 26112, 26111) had egg complements of 18 and 20 eggs respectively.

Distribution.—Known only from the Andean cordillera Oriental west of the Río Apurimac and Cordillera Vilcabamba in Depto. Ayacucho, Perú, between 2460 and 2650 m (Fig. 4). A single specimen was evidently collected at 1650 m.

Remarks.—*P. pereger* is probably most closely allied to *P. parkeri.* Both have the most T-shaped terminal phalanges of the species of the *flavomaculatus* group. The two species are readily separable in that the tympanum is visible in *pereger* and concealed in *parkeri,* the snout is rounded in *pereger* whereas it is sloping in lateral profile in *parkeri,* and the parasphenoid is shorter in *pereger* (not reaching the palatines) than in *parkeri* (Fig. 10). The two frogs are about the same size and have similar proportions.

The discovery of a *flavomaculatus* group species so far south in Perú suggests that there are probably several other populations distributed along the higher elevations of the Amazonian versant of the Cordilleras Central, Oriental, and possibly Vilcabamba. Once these populations become known, it may prove to be the case that *flavomaculatus, parkeri,* and *pereger,* are merely vicariant populations now separable in our ignorance.

Phrynopus peruanus Peters

Phrynopus peruanus Peters, 1874:416 (Type–locality.—Maraynioc, Depto. Junín, Perú; *holotype not seen by author*).
Borborocoetes peruanus—Boulenger, 1882:255.
E[upsophus] peruanus—Parker, 1932:344.

Diagnosis.—A moderate–sized *Phrynopus* (♀♀ 23.3–30 mm SVL); skin of dorsum and venter smooth with scattered low pustules; first finger shorter than second; digit tips not bulbous; toes lacking lateral fringes and webbing; two metatarsal tubercles, equal in size; tarsus lacking tubercles or folds; tympanum visible, prominent, its length 2/5–1/2 that of eye; snout rounded in lateral profile; prevomerine teeth present on small odontophores posteromedial to choanae; frontoparietals complete, lacking prominent crests; nasals large, separated medially; anterior ramus of parasphenoid long, not reaching palatines; medial pterygoid ramus widely separated from parasphenoid ala; brown above and below; venter may be reticulated with dark brown.

Description (based on 2 females).—Head narrower than body, longer than wide; head width 32.2–38.2 % SVL; snout subacuminate to rounded in dorsal view, rounded to weakly sloping in lateral profile; snout short, E–N 59.1–63.6 % eye length; canthus rostralis sharp, concave; nostrils not protuberant, directed laterally; loreal region concave, sloping gradually to lips; lips not flared; interorbital space flat (no frontoparietal crests), broad, upper eyelid width 74.4 % IOD; upper eyelid not tuberculate; supratympanic fold present, glandular, not obscuring tympanum; tympanum visible, higher than long, its length 41.8–52.3 % eye length; choanae small, wider than long, slightly larger than a prevomerine odontophore, at edge of palate but not concealed by palatal shelf of maxillary arch; prevomerine odontophores well posterior and slightly medial to choanae, bearing a clump of 2–4 teeth; tongue longer than wide, not notched posteriorly, posterior one–half not adherent to floor of mouth; males not seen.

Skin of dorsum smooth with low scattered warts (not areolate); dorsum not bearing ridges or folds; skin of venter smooth; discoidal folds obscure, well posterior on venter; no ulnar tubercles or folds; one or two palmar tubercles (when two are present, outer is no larger than a supernumerary tubercle); larger palmar tubercle round, twice size of elongate thenar tubercle; a few supernumerary tubercles distal to palmar tubercle(s); subarticular tubercles broader than long, low, flat, non-conical; fingers lacking fringes or webbing; fingers lacking pads or discs, not dilated apically; first finger slightly shorter than second.

Shank 31.2–33.0 % SVL; no tarsal or heel tubercles; two prominent metatarsal tubercles, both longer than wide, equal in size; no supernumerary plantar tubercles; subarticular tubercles round, low, flat, non-conical, smaller than those of fingers; toes not fringed or webbed, tips not bulbous, lacking pads or discs.

In preservative, *P. peruanus* is brown above and below; the venter is paler than the dorsum. The limbs are not or only feebly

barred and the dorsal pattern, if present, consists of indefinite flecking of darker brown. A canthal stripe may be present or not. The lips are not barred. The venter is uniform brown with occasional cream flecks to creamy-brown with brown reticulation.

Distribution.—Known only from the type-locality, Maraynioc, Depto. Junín, Perú (Fig. 14).

Remarks.—I have seen only two specimens of this species. The smaller individual was partially dissected in order to gain some knowledge of the skeletal features of this species. The frontoparietal bones are complete and no fontanelle is exposed. The frontoparietal bones are not in contact with the nasal bones. The latter are relatively large and distinctly separated. The sphenethmoid is large and extensive, paralleling the situation illustrated for *P. peraccai* (Lynch, 1968, as *Niceforonia festae*) or *P. montium* (Lynch, 1971, as *Niceforonia montium*). The palatal process of the premaxilla is very long. The prevomers resemble those of *P. montium* except that odontophores are present and bear teeth. The parasphenoid of *P. peruanus* is like that of *P. montium*. The medial ramus of the pterygoid is shorter in *P. peruanus* than in *P. montium*. The occipital condyles are not stalked and are widely separated in *P. peruanus*.

Osteologically, *P. peruanus* is very similar to *P. laplacai*, *P. montium*, and *P. wettsteini*, but is easily differentiated in retaining prevomerine teeth. The external features of *P. peruanus* do not readily support this association. The nearly smooth skin of *P. peruanus* suggests association with the frogs of the *flavomaculatus* group or with *P. peruvianus*. However, all of these species have a thumb that is longer than the second finger. The apparently smooth skin of *P. peruanus* may be an artifact of preservation. The areolations lateral and ventral to the anus are nearly obliterated in the specimens available to me. This suggests to me that the skin texture on the venter and dorsum of the specimens I have seen may not be reflective of the condition in living or carefully preserved frogs. Peters' (1874) characterization of the skin texture as "*etwas uneben*" suggests that the skin texture of his specimens was not clearly smooth or areolate. At present, I consider *P. peruanus* closely related to *P. laplacai*, *P. montium*, and *P. wettsteini*.

Phrynopus peruvianus (Noble), new combination

Sminthillus peruvianus Noble, 1921:1 (*Holotype.*—AMNH 14526, near Juliaca, Depto. Puno, Perú).
Noblella peruviana—Barbour, 1930:81.
(*Eleutherodactylus*) *peruvianus*—Lynch, 1971:148.

Diagnosis.—A small *Phrynopus* (♂♂ 16.4–21.7 mm, ♀♀ 20.6–25.1 mm SVL); skin of dorsum and venter smooth; first finger slightly longer than or equal to second; fingers and toes with bulbous tips; toes without lateral fringes and basal webbing; two metatarsal tubercles, inner slightly larger than or equal to outer; inner tarsal tubercle present; tympanum present, concealed (partially) beneath skin; snout truncate in lateral profile; males with vocal sac and slits;

prevomerine teeth, dentigerous processes, and dentigerous ramus of prevomer lacking; frontoparietals complete, not bearing crests; nasals widely separated; anterior ramus of parasphenoid not reaching palatines; dorsum gray to brown, blotched with dark brown; venter dark brown flecked with cream; throat of males dull gray–brown.

Description.—Head narrower than body (Fig. 17), slightly wider than long; head width 34.4–40.4 ($\bar{x} = 36.6$) % SVL in ♂♂, 32.9–36.5 ($\bar{x} = 34.7$) in ♀♀; snout subovoid in dorsal view, truncate in lateral profile; tip of snout extends further anteriad than anterior edge of upper jaw; canthus rostralis sharp, concave; loreal region concave, sloping abruptly to lip; lips not flared; nostrils not protuberant, directed laterally; snout short, E–N slightly less than to equal to eye length; interorbital region flat, upper eyelid width 66.4–86.3 ($\bar{x} = 76.6$) % IOD in ♂♂, 71.5–93.8 ($\bar{x} = 81.2$) in ♀♀; supratympanic fold glandular, not prominent; tympanum present, concealed beneath skin but evidenced externally by a depression in the temporal region; postrictal tubercles prominent; choanae small, round, situated well anterolaterally on palate, concealed by palatal shelf of maxillae when roof of mouth is viewed from directly above; prevomerine teeth and dentigerous processes lacking; tongue narrow, much longer than wide, not notched posteriorly, posterior one–fourth free; males with short, posterolateral vocal slits and a median, external, subgular vocal sac (Fig. 17).

Skin smooth except for postrictal tubercles and scattered warts on flanks, posteroventral surfaces of thighs, and tarsus; dorsolateral folds are weakly evident in scapular region; no discoidal folds; forearm lacking ulnar tubercles; palmar tubercle not bifid, larger than thenar tubercle; palmar surface with a few prominent supernumerary tubercles (Fig. 7); subarticular tubercles of fingers round, flat, simple; fingers lacking lateral fringes; tips of fingers bulbous, lacking pads; first finger slightly longer than second, or equal in length to second.

Heel lacking tubercles; outer edge of tarsus bearing a row of weakly developed tubercles; inner edge of tarsus bearing a prominent, elongate, sigmoid–shaped tubercle (Fig. 8) not contiguous with inner metatarsal tubercle; two metatarsal tubercles, both prominent and subconical, inner slightly larger and longer than wide, outer round; subarticular tubercles of toes conical, round, simple; toes without lateral fringes and basal webbing; tips of toes bulbous, lacking pads; hind limb short, heel of adpressed limb reaches to between tympanum and posterior edge of eye; shank 38.2–45.2 ($\bar{x} = 42.9$) % SVL in ♂♂, 38.0–46.0 ($\bar{x} = 41.7$) in ♀♀.

In preservative the ground color is usually gray to brown with dark brown markings; one individual is dull yellow above with dark brown markings. The dorsal pattern is irregular and variable. Eleven individuals have a mottled dorsum with no distinct pattern. Ten others have a broad middorsal yellow stripe and a disruption

of the brown markings which form a dark brown border with irregular edges (see Noble's, 1921, Fig. 2); the dorsal stripe bifurcates at the vent and continues along the posterior surface of the thigh. Thirty-seven others have a dorsal pattern of an interorbital triangle, a large scapular X, and a sacral chevron.

The flanks and sides of the head are darker than the dorsum and the facial markings consist of a canthal stripe, supratympanic stripe, and labial bars. The limbs are barred and the bars are as wide as the paler interspaces. All markings are edged with cream. Seventeen specimens have a hairline middorsal stripe from the sacrum to the vent. The posterior surface of the thighs is black. The venter is dull brown to black and weakly to heavily flecked with pale cream. The throat is darker than the venter and rarely flecked with cream. In the specimens with a broad middorsal stripe, the venter has a sagittal stripe with a crossbar in the pectoral region; the ventral lines are cream.

In life, the ground color varies from dull brown, tan, tan–orange, to reddish and if bearing dorsal markings, they are dull red, tan, or gray. The venter is bluish–gray with brown reticulations. The throats of the males are dull grayish–brown. The middorsal stripe, when present, is orange–yellow. The iris is dark brown with gold flecks.

Natural history.—The KU specimens were collected beneath rocks in ravines within the *puna*. In the ravines, shrubby vegetation (2 m in height) was found. Most specimens of *peruvianus* were found beneath moss–covered rocks in seepage areas within the ravines. The adult females are gravid and calling males were encountered on the afternoon of 16 January 1971. The call was described as "a series of short, quickly repeated, moderately high notes, resembling a slow–calling *Pseudacris triseriata*" (William E. Duellman field notes 16 January 1971). The altitudinal range of the KU specimens is from 3270 m to 3450 m.

Distribution.—*Phrynopus peruvianus* is known only from the localities cited in the appendix. The Abra Acanacu is a pass in the Cadena del Paucartambo on the northwestern end of the Cordillera Carabaya. The localities lie in moist paramo in contrast to the stark habitat seen around Juliaca (Puno). Dr. Thomas Fritts is of the opinion that Keays' collection was made in the more mesic habitats to the northeast of Juliaca and may have come from a broad assortment of habitats, elevations and localities in southern Perú (Fig. 14).

Remarks.—*Phrynopus peruvianus* is osteologically isolated from the other species of the genus. The extensive reduction of the prevomers and fused pectoral girdle readily distinguish it from all other species. No other species has a tarsal tubercle but the other external features of *P. preuvianus* are not especially distinctive. In view of the variation prevomers (especially reduction) seen else-

where among frogs, I am not willing to use that trait in conjunction with the pseudofirmisterny to generically distinguish *peruvianus;* in other respects the species is too similar to other southern Andean simple-toed eleutherodactylines.

Phrynopus simonsii (Boulenger), new combination

Paludicola simonsii Boulenger 1900:182 (Cotypes.—BMNH RR 1947.2.15.43–44, paramo; here restricted to 8 km E Cajamarca, Depto Cajamarca, Perú, 3000 m; BMNH 1947.2.15.43 is here designated the Lectoholotype of *Paulicola simonsii* Boulenger).

Syrrhophus simonsii—Parker, 1927:451.

Niceforonia simonsii—Lynch, 1968:291.

Diagnosis.—A moderate-sized *Phrynopus* (single adult female 30 mm SVL); skin of dorsum and venter areolate; dorsolateral folds present; first finger shorter than second; digital tips bulbous; toes bearing lateral fringes and basal webbing; two metatarsal tubercles, inner twice as large as outer; tarsus lacking tubercles, indefinite inner tarsal fold present; tympanic annulus, columella, and cavum tympanum absent; snout rounded in lateral profile; prevomerine teeth and dentigerous processes absent, dentigerous ramus present, large; frontoparietals complete, lacking crests; nasals large, narrowly separated; anterior ramus of parasphenoid in contact with palatines; dorsum tan, flanks spotted with brown, groin with vertical brown bars, venter cream.

Description of the lectoholotype (BMNH 1947.2.15.43).—Head as wide as body, as wide as long, head width 35.4 % SVL; snout subacuminate in dorsal view, rounded in lateral profile (Fig. 4); canthus rostralis sharp, slightly concave; loreal region weakly concave, sloping abruptly to non-flared lips; nostrils not protuberant, directed dorsolaterally, much closer to tip of snout than to eye; snout short, eye length greater than E–N; interorbital region flat, no cranial crests; width of upper eyelid 93.3 % IOD; supratympanic fold prominent; tympanum absent; tongue large, thick, fleshy, not notched posteriorly, posterior one-half free; prevomerine teeth and dentigerous processes absent; choanae small, completely visible when roof of mouth is viewed from directly above, just inside palatal shelf of maxillae.

Skin of head and dorsum warty, at present warts are loosely defined; glandular dorsolateral folds present from scapular region to above groin; skin of limbs warty, venter areolate, throat less areolate; skin on anterior surface of thighs smooth; shank 36.7 % SVL; heel of adpressed limb reaches to posterior edge of head; forearm bearing indefinite ulnar ridge; three palmar tubercles, outer poorly defined (Fig. 6); no supernumerary thenar tubercles; subarticular tubercles low, flat, round, simple; fingers lacking lateral fringes; first finger shorter than second; tips of fingers swollen into pad-like structures.

Inner edge of tarsus bearing indefinite fold; outer edge of tarsus and heel lacking tubercles or folds; two metatarsal tubercles, inner twice as large as outer, both ovoid, not compressed, non-conical;

plantar surface bearing indefinite supernumerary tubercles; subarticular tubercles low, round, flat, simple; toes bearing lateral fringes and basal webbing; tips of toes bulbous.

The ground color is tan. The flanks are spotted with brown and on the upper flank is an elongated dark brown stripe–like spot. The supratympanic fold is edged with brown. The venter is dirty cream without spotting or reticulations. The groin is marked with a dark brown vertical bar against a cream background. Dark brown patches are present behind the knee and inside the heel. The limbs are not barred.

Distribution.—Known only from the type–locality (Fig. 14). During my stay at the British Museum I examined correspondence between P. O. Simons, the collector, and Dr. Oldfield Thomas, then curator of mammals and director of the British Museum. In a letter from Simons to Thomas dated 20 November 1899, Simons refers to a paramo locality some 5 miles east of Cajamarca. The type–locality is here revised from "Paramo, Cajamarca" to 8 km E Cajamarca.

Remarks.—Three species of *Phrynopus* lack ears (*cophites, nanus, and simonsii*). The three also agree in having the first finger shorter than the second, and in having coarsely areolate skin on the venter. Although *nanus* differs from *cophites* and *simonsii* in having visible dentigerous processes on the prevomer, I consider *nanus* and *simonsii* closely related. The limited knowledge of the osteology of *nanus* and *simonsii* reveals considerable similarity in contrast to the marked dissimilarity of *cophites*. The osteological data suggests that *simonsii* is more closely allied to the frogs of the *flavomaculatus* group than to the more southern *peruanus* group (which it resembles in external characteristics).

Phrynopus wettsteini (Parker), new combination

Eupsophus wettsteini Parker 1932:43. (*Holotype.*—NMW 15845, Untuaro or Pongo, possibly Depto. Amazonas, Perú, 2000 m. Not *examined by author*). *Niceforonia wettsteini*—Lynch, 1969:273.

Diagnosis.—A small to moderate–sized *Phrynopus* (known specimens 21–28 mm SVL); skin of dorsum and venter areolate; first finger shorter than second; tips of fingers not bulbous; toes lacking lateral fringes and basal web; two metatarsal tubercles, inner much larger than outer; tarsus lacking tubercles or folds; tympanum partially concealed beneath skin; snout rounded in lateral profile; males with vocal sac and slits; prevomerine teeth and dentigerous processes lacking, dentigerous ramus of prevomer present; frontoparietals complete, lacking crests; nasals narrowly separated; anterior ramus of parasphenoid short, not reaching palatines; dorsum dark brown, venter brown with darker reticulations; throat black.

Descriptions.—See Parker (1932).

Distribution.—Known only from the type–locality, presumably on the Amazonian slopes of one of the Andean Cordilleras (Fig. 14).

Remarks.—The only specimen of this species which I have examined in detail relative to its relationships to other *Phrynopus*

species is the cleared and stained example. Although the other four paratypes were studied, my notes on them deal only with the generic affinities of this small frog and my data are thus inadequate for species-level comparisons.

Osteologically, *P. wettsteini* agrees well with *P. laplacai* and *P. montium*, both of which occur at much higher elevations than that recorded for *P. wettsteini*. There is considerable external similarity between these three frogs as well. The principal differences, judging from the unsatisfactory position of small samples, involve relative sizes of the metatarsal tubercles, relative lengths of the inner two fingers, and coloration. Aside from the striking altitudinal and geographic differences in type-localities, and the very small samples available, I might argue that all three are conspecific.

The type-locality of *P. wettsteini* is not known with certainty. Dr. Josef Eiselt informed me that in the records at Vienna, the word "Pongo" was associated with or situated near Borja, a small town on the Rio Marañon near the frontier between Depto. Amazonas and Loreto. The mountains in that vicinity reach 2000 m and the type-locality of *wettsteini* is presumed to be in the vicinity of Borja.

One other nominate species has been referred to this generic grouping—*Borborocoetes columbiana* Werner. The holotype of the species is now lost and no other specimens have been assigned to the species. If Werner's (1899) description and my inferences from the description concerning character states not specifically mentioned by Werner are accurate, the frog may be a *Phrynopus* allied to *P. brunneus* and *P. peraccai*. A partial diagnosis of the frog is presented below; the character states in italics are suppositions on my part, not data given by Werner.

Phrynopus columbianus (Werner), new combination

Borborocoetes columbiana Werner 1899:480 (Holotype now lost; Monte Redondo, Buenavista, Depto. Cundinamarca or Meta, Colombia, 1000–1300 m).

Niceforonia columbiana—Lynch, 1968:292.

Diagnosis.—A small *Phrynopus* (an individual of unknown sex and age, 18 mm SVL); *skin of dorsum warty, that of venter smooth;* first finger equal in length to second; *fingers and toes not dilated at tips;* toes basally webbed; inner metatarsal tubercle small, outer absent (*unlikely; outer probably obscure but much smaller than inner); inner edge of tarsus lacking tubercle;* tympanum prominent, ⅔ length of eye; snout rounded or truncate in lateral profile; *prevomerine dentigerous processes present, posteromedial to choanae;* dorsum dark brown with little or no pattern other than pale interorbital bar; venter white with brown reticulation.

Remarks.—Cochran and Goin (1970) and Werner (1899) suggested that the frog was immature; the suggestion is based on the small size of the type. However, it may be an adult (*nanus* and *peraccai* are only slightly larger frogs). If the frog is a *Phrynopus*, it is most similar to the two Ecuadorian species found at higher

elevations on the Amazonian versant of the northern Andes (*P. brunneus* and *P. peraccai*). I doubt that it is identical to either of the Ecuadorian species; this conclusion is based on Werner's (1899) description of the color pattern and the purported presence of basal webbing of the toes of the holotype.

INTRAGENERIC RELATIONSHIPS

If *P. columbianus* is included, the genus *Phrynopus* contains fourteen nominate species distributed in the Andes from northern Colombia to western Bolivia at elevations of 1000–4000 m (Fig. 18). A single case of sympatry is known (*P. cophites* and *P. peruvianus*) for the otherwise dispersely distributed genus. The relationships of the frogs of the genus *Phrynopus* to other eleutherodactylines are obscure, but the genus is probably most closely related to *Eleutherodactylus* (Lynch, 1971). The simple digits characteristic of *Phrynopus* could represent the primitive character state for eleutherodactyline frogs or may represent a retrograde evolutionary step. The digital character state seen in several *Phrynopus* species (no discs, terminal phalanges intermediate between knobbed and T-shaped) could support either argument.

The fourteen species are divided into four species groups; these are defined below:

flavomaculatus group: first finger longer than second; skin smooth; toes lacking lateral fringes and basal webbing; no tarsal tubercle; prevomerine teeth present on processes lying posteromedial to choanae; median pterygoid ramus in contact with parasphenoid ala; anterior parasphenoid ramus in contact (or nearly so) with palatines; ear fully developed; pectoral girdle functionally arciferal. Frogs of this group also have comparatively large nasal bones.

Content: *P. brunneus, P. columbianus, P. flavomaculatus, P. parkeri, P. peraccai, and P. pereger.*

peruvianus group: first finger as long as second (or slightly longer); skin smooth; toes lacking lateral fringes and basal webbing; inner tarsal tubercle present; prevomerine teeth, dentigerous processes, and dentigerous ramus absent; pterygoid not in contact with parasphenoid; anterior parasphenoid ramus short, not reaching palatines; ear fully developed; pectoral girdle functionally firmisternal. The nasal bones are relatively small and widely separated medially.

Content: *P. peruvianus.*

simonsii group: first finger shorter than second; skin areolate; toes bearing lateral fringes and basal webbing; no tarsal tubercle; prevomerine teeth and processes present (*nanus*) or absent (*simonsii*), when absent, dentigerous ramus not reduced in size;

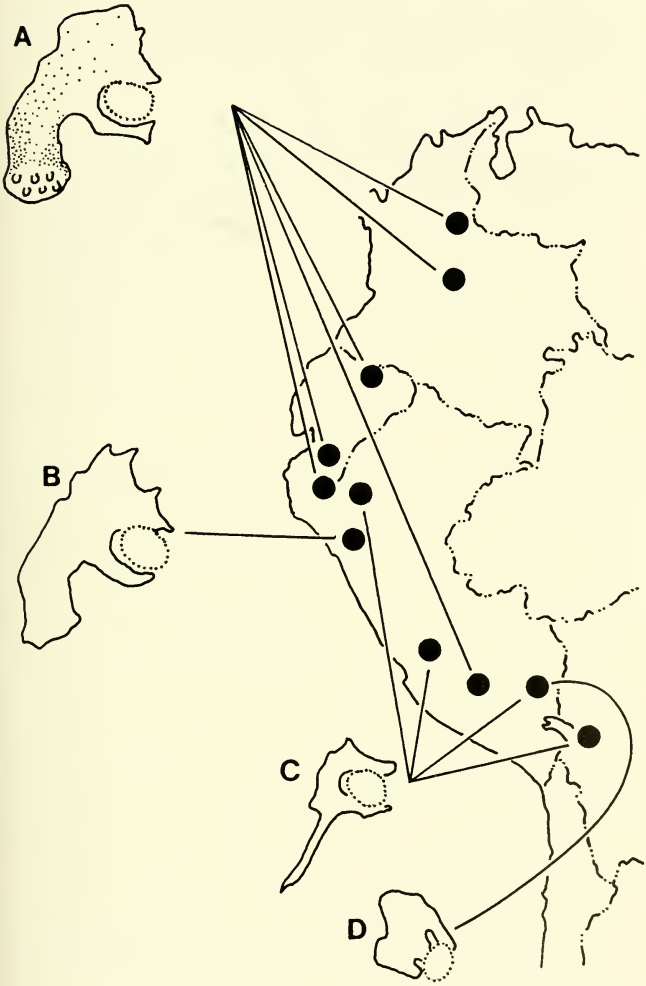

FIG. 18.—Clinal variation in prevomerine bones in *Phrynopus*. (A,B) *flavomaculatus* and *simonsii* groups, (C) *peruanus* group, and (D) *peruvianus* group.

median pterygoid ramus in contact with parasphenoid ala (*simonsii*); anterior parasphenoid ramus long, in tenuous contact with palatines (*simonsii*); ear absent (possibly only greatly reduced in *nanus*); pectoral girdle functionally arciferal. The nasals are large and in contact or narrowly separated.

Content: *P. nanus* and *P. simonsii.*

peruanus group: first finger not longer than second (usually shorter); skin areolate (condition uncertain in *peruanus*, see description); toes lacking lateral fringes and basal webbing; no tarsal tubercle; prevomerine teeth and dentigerous processes lacking (except in *peruanus*), dentigerous ramus thin and sliver-like; median pterygoid ramus narrowly (*laplacai, montium, peruanus, wettsteini*) or broadly (*cophites*) separated from parasphenoid ala; anterior parasphenoid ramus short, not reachin palatines; ear fully developed (except *cophites,* ear absent); pectoral girdle functionally arciferal. The nasal bones are moderate–sized and narrowly separated.

Content: *P. cophites, P. laplacai, P. montium, P. peruanus,* and *P. wettsteini.*

On the basis of external characteristics (including those of the mouth), I consider the *flavomaculatus* and *peruvianus* groups more similar to one another than to the other two species groups, which form a compact unit. The osteological data suggest that the *flavomaculatus* and *simonsii* groups are closely related and that *peruvianus* and *peruanus* groups are closely related. This lack of concordance is suggestive that the genus *Phrynopus* may not be diphyletic but that early in its evolution gave rise to two lineages, one leading to the *flavomaculatus* group and the second giving rise to the predominantly southern component.

In an attempt to test my subjectively determined grouping of *Phrynopus,* I analyzed the intrageneric relationships with the method described by Camin and Sokal (1965). Eleven characteristics (number 1–11), each with two to four character–states, were used. Data are incomplete for three species (*P. columbianus, P. nanus,* and *P. peruanus*) and these taxa have accordingly been excluded from the analysis. The characteristics, character–states, and coding (0 = primitive, 1 or 1′ derived, 2 derived from 1, and 3 derived from 2) are listed below:

1.—Prevomers. Four character–states. 0: prevomer large, toothed; 1: prevomer large, toothless; 2: prevomer moderate–sized, edentate or not, dentigerous ramus thin (sliver–like); 3: prevomer minute, dentigerous ramus lost.

2.—Ears. Two character–states. 0: ear present, visible or concealed; 1: ear absent.

3.—Frontoparietals. Three character–states. 0: no cranial crests,

no fontanelle (complete frontoparietals); 1: no cranial crests, fontanelle present; 1′: cranial crests present, no fontanelle.

4.—Parasphenoid ala. Three character–states. 0: ala in contact with median pterygoid ramus: 1: ala narrowly separated from median pterygoid ramus; 2: ala widely separated from median pterygoid ramus.

5.—Anterior parasphenoid ramus. Two character–states. 0: not reaching palatines; 1: in contact with palatines.

6.—Nasal bones. Two character–states. 0: large nasals, in broad median contact; 1: nasals smaller, narrowly to relatively widely separated medially.

7.—Skin of venter. Two character–states. 0: texture smooth; 1: texture coarsely areolate.

8.—Finger lengths (I and II). Two character–states. 0: thumb longer than second finger; 1: thumb not longer than second finger, usually shorter.

9.—Toe fringes. Two character–states. 0: present; 1: absent.

10.—Snout shape. Two character–states. 0: rounded or truncate in lateral profile; 1: sloping in lateral profile.

11.—Metatarsal tubercles. Two character–states. 0: outer metatarsal tubercle much smaller than inner; 1: outer metatarsal tubercle more than one–half size of inner (equal in most cases).

Because both derived character–states of character 3 are unique (*i.e.*, a derived character–state is evident in less than two taxa), characteristic 3 was not used in the analysis. The derived states are indicated on the cladogram (Fig. 19) by a dash accompanied by the number of the characteristic. In determining evolutionary direction within characteristics, I considered widespread character states ("normal" among frogs as a whole, but especially among the archaic groups) as well as character states occurring in putative primitive eleutherodactyline genera (*viz.*, *Hylactophryne* and *Ischnocnema*) to be primitive character–states. Those character states found among *Phrynopus*, but not seen in the species of more primitive telmatobiines (Grypiscini, Telmatobiini, Batrachylini, Odontophrynini) or among most eleutherodactylines, are considered to be derived.

Inspection of the cladogram (Fig. 19) reveals a concordance of groupings to those proposed above (*flavomaculatus*, *peruanus*, and *simonsii* species groups) in the cladogram using subcladograms A or A′, and B. Using the equally parsimonious subcladogram B′ requires considering the *peruvianus* and *peruanus* groups not defensibly separable on the basis of the characteristics and character–states employed here. Subcladogram B emphasizes characteristic 11 (metatarsal tubercle size) at the expense of an extra evolutionary step for characteristics 4 and 8; subcladogram B′ emphasizes 8 (finger lengths) at the expense of extra steps for 4 and 11; emphasis

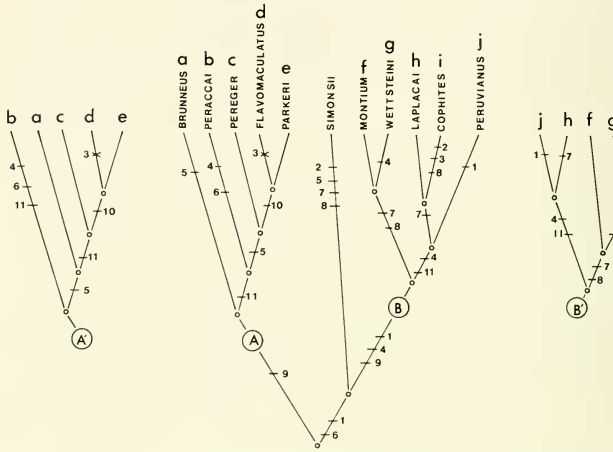

FIG. 19.—Most parsimonious cladogram (27 evolutionary steps) for eleven species of *Phrynopus*. Equally parsimonious subcladograms for the *flavomaculatus* group (A', upper left) and the *peranus–peruvianus* groups (B', top right) are also illustrated. The dashes across lines (and the attending number) represent evolutionary shifts from a primitive to a derived character state.

of characteristic 4 or 7 results in less parsimonious cladograms (the number of steps is increased from 27 to 28).

My preference among the equally parsimonious cladograms is subcladogram B, as indicated in the recognition of a *peruvianus* group. In support of this, I cite the functionally firmisternal pectoral girdle of *peruvianus*, a feature not duplicated elsewhere in the genus, and the likewise extensive reduction of the prevomers.

INTERGENERIC RELATIONSHIPS

In the course of my studies of South American *Eleutherodactylus*, I have concluded that there are two major groupings of South American species—(1) the *binotatus* and *fitzingeri* groups, containing those frogs having the first finger longer than the second and having smooth or feebly granulate skin of the venter, and (2) the *unistrigatus* group, containing species having the first finger much to slightly shorter than the second and having coarsely areolate skin on the venter. In excess of 95% of the nominate species from South America fall into the two contingencies. The species of the *Phrynopus flavomaculatus* group bear considerable external as well as osteological similarity to the frogs of *Eleutherodactylus binotatus* group. The recently described *E. elassodiscus* (Lynch, 1973) is almost perfectly annectant between other narrow-toed

species of the *E. binotatus* group and the larger species of the *P. flavomaculatus* group, except that it has digital discs as do other *Eleutherodactylus*. The similarity between these frogs is so extensive that I am convinced that the *P. flavomaculatus* group is an upland derivative of the *E. fitzingeri* group (a predominantly lowland group—below 1000 m).

Parker's (1932) suggestion that some of these frogs (the *simonsii* and *peruanus* groups) were derived from a "*Borborocoetes*" group of *Eleutherodactylus* is plausible if the two groups of *Eleutherodactylus* mentioned above are natural groups. The *E. unistrigatus* group and the *P. simonsii* and *P. peruanus* groups agree in relative finger lengths and the texture of the skin of the venter. In addition, many of the Andean species of the *E. unistrigatus* group in southern Ecuador have narrowly separated nasal bones, as do the frogs of the *P. peruanus* group. Several high-altitude species of the *E. unistrigatus* group have reduced digital pads and small prevomerine dentigerous processes (thus approaching the *P. simonsii* and *P. peruanus* groups), but differ in having discs on the digits.

One difficulty with deriving the *flavomaculatus* group from the *E. fitzingeri* group and the *simonsii* and *peruanus* groups from the *E. unistrigatus* group is the disposition of *P. peruvianus*. Osteologically, *P. peruvianus* is much more similar to the frogs of the *P. peruanus* group than to the *P. flavomaculatus* group or the *P. simonsii* group, whereas, on the basis of external characteristics, *P. peruvianus* more closely resembles the frogs of the *P. flavomaculatus* group. The lack of concordance between species groups of *Phrynopus* and the major groups of South American *Eleutherodactylus* does not support the idea that *Phrynopus* is diphyletic. Although I have not yet examined the assumption cladistically, I assume *Phrynopus* to be derived from an *Eleutherodactylus* stock not unlike the group of species now represented by *E. cruralis, E. elassodiscus, E. granulosus,* and *E. nigrovittatus*. This complex of species occurs along the eastern base of the Andes in Ecuador and in southern Peru and adjacent Bolivia.

SUMMARY

The Andean eleutherodactyline frogs having narrow heads and lacking digital discs are placed in the genus *Phrynopus*. The genera *Niceforonia* and *Noblella* are synonyms. Fourteen species are recognized; five of them are named as new species. *Phrynopus brunneus* is named from the high Amazonian Andean slopes (valley of the Rio Chingual) in Ecuador. *Phrynopus peraccai* is named from the high Amazonian Andean slopes (valley of the Rio Papallacta) in Ecuador; this species was previously known as *Niceforonia festae*. *Phrynopus parkeri* is named from a mountain crest in the Huancabamba pass in northern Perú. *Phrynopus pereger* is named from

intermediate elevations on the eastern slopes of the Cordillera Oriental in south-central Perú. *Phrynopus cophites* is named from high elevations in the Cordillera Carabaya in southern Perú.

Four species groups are recognized. The *flavomaculatus* group includes six species (*brunneus, columbianus, flavomaculatus, parkeri, peraccai,* and *pereger*), five occurring in central Colombia, Ecuador, and extreme northern Perú, and one (*pereger*) found in southern Perú. The generotype of *Noblella* (*peruvianus*) is the only species included in the *peruvianus* group (southern Perú). The *simonsii* group included *nanus* (generotype of *Niceforonia*) from north–central Colombia and *simonsii* from northern Perú. The *peruanus* group includes five species, four from southern Perú and Bolivia (*cophites, laplacai, montium* and *peruanus*) and one apparently found on the Amazonian slopes of northern Perú (*wettsteini*).

Some characteristics used to distinguish genera exhibit variation among the species of *Phrynopus.* Three species (*cophites, nanus,* and *simonsii*) lack ears. Prevomerine teeth and odontophores are absent in the species of the *peruvianus* and *peruanus* groups as well as in *simonsii,* but are uniformly present in species of the *flavomaculatus* group. One species (*cophites*) has a large frontoparietal fontanelle; one other species (*flavomaculatus*) has prominent cranial crests. *Phrynopus peruvianus* is unique in having a functionally firmisternal pectoral girdle.

The distribution of *Phrynopus* is diperse. A single case of sympatry is known (*cophites* and *peruvianus*). Only *flavomaculatus* is known to occur over any modest area; the other thirteen species occur at single localities or at a few clustered localities. A major distributional gap occurs from northern Perú to central Perú and many additional populations are expected in the 600 kilometer distributional hiatus.

RESUMEN

Las ranitas andinas eleutherodactilinas que tienen la cabeza angosta y carecen de discos digitales se colocan en el género *Phrynopus.* Los géneros *Niceforonia* y *Noblella* son sinónimos. Se reconocen catorce especies dentro de este grupo de ranitas, cinco de las cuales son nuevas para la ciencia. Se nombra a *Phrynopus brunneus* de las faldas andinas altoamazónicas del Ecuador (Valle del Río Chingual). Se nombra a *P. peraccai* de las faldas andinas altoamazónicas del Ecuador (Valle del Río Papallacta); esta especie se le conoció previamente como *Niceforonia festae.* Se nombra a *Phrynopus parkeri* de la cresta montanosa del paso Huancabamba en el norte de Perú. Se nombra a *Phrynopus pereger* de elevaciones intermedias en las faldas del este de la Cordillera Oriental del sur–centro de Perú. Se nombra a *Phrynopus cophites* de las altas elevaciones de la Cordillera Carabaya en el sur de Perú.

Se reconocen cuatro grupos de especies. El grupo *flavomaculatus* incluye seis especies (*brunneus, columbianus, flavomaculatus, parkeri, peraccai,* y *pereger*), cinco se distribuyen en el centro de Colombia, Ecuador, y en el extremo norte de Perú, y una (*pereger*) se encuentra en el sur de Perú. El generotipo de *Noblella* (*peruvianus*) es la única especie que se incluye en el grupo *peruvianus* (sur de Perú). El grupo *simonsii* incluye a *nanus* (generotipo de *Niceforonia*) de la parte nor-central de Colombia y a *simonsii* del norte de Perú. El grupo *peruanus* incluye cinco especies, cuatro del sur de Perú y Bolivia (*cophites, laplacai, montium,* y *peruanus*) y una que aparentemente se encuentra en las faldas amazónicas del norte de Perú (*wettsteini*).

Algunas de las características usadas para separar a los géneros muestran variación entre las especies de *Phrynopus*. Tres especies carecen de oido (*cophites, nanus,* y *simonsii*). Las especies de los grupos *peruanus* y *peruvianus,* asi como del grupo *simonsii,* carecen de dientes prevomerianos y odontoforos, pero están presentes en las especies del grupo *flavomaculatus*. Una especies (*cophites*) tiene una fontanela frontoparietal grande; otra especie (*flavomaculatus*) tiene crestas craneales prominentes. *Phrynopus peruvianus* sobresale del resto de las especies por tener una cintura pectoral firmisterna funcional.

La distribución geográfica de *Phrynopus* es dispersa. Solo se conoce un caso de simpatridas (*cophites* y *peruvianus*). Solamente *flavomaculatus* presenta una distribución modesta; las otras trece especies se conocen de una sola localidad o de pocas pero muy juntas unas de las otras. Hay gran discontinuidad distributiva desde el norte hasta el centro de Perú, y es de esperarse muchas poblaciones adicionales en este hiato de 600 kilómetros.

APPENDIX: SPECIMENS EXAMINED

Phrynopus brunneus.—ECUADOR: *Carchi:* 10 km WNW El Carmelo, 3150 m, USNM 192909–12.

Phrynopus cophites.—PERÚ: *Cuzco:* S slope Abra Acanacu, 14 km NNE Paucartambo, 3400 m, KU 138884; N slope Abra Acanacu, 27 km NNE Paucartambo, 3450 m, KU 138885–908, 138909–10 (cleared and stained skeletons), 138911–16; N slope Abra Acanacu, 29 km NNE Paucartambo, 3400 m, KU 138918.

Phrynopus flavomaculatus.—ECUADOR: *Loja:* 13.2 km E Loja, 2770 m, KU 141474; 13 5 km E Loja, 2800 m, KU 141475; 15 km E Loja, 3000 m, BMNH 1947.2.16.11–15; 8–9 km N San Lucas, 3000–3100 m, KU 119737–42, 121354 (eggs); 10 km S Saraguro, 3100 m, KU 142201–02. *Morona-Santiago:* San Juan Bosco, 2215 m, USNM 195393–994; between Sevilla de Oro and Mendez, 2460–2580 m, USNM 195395, 195425–27; between Suro Rancho and Sapote, 2650 m, USNM 195396–97; Suro Rancho, 2710 m, USNM 195398–411; ½ km W Suro Rancho, 2770 m, USNM 195412–17; San Vicente, 2860 m, USNM 195418, 195419 (cleared and stained skeleton), 195420–23; Cerro Negro, 2950 m, USNM 195424. *Zamora-Chinchipe:* 13–14 km E Loja, 2800 m, KU 119721–24, 119743 (cleared and stained skeleton); 14 km E Loja,

2780 m, KU 141476–77; 15 km E Loja, 2710 m, KU 142198–200; 15 km E Loja, 2800 m, KU 119716–20, 119725–36.

Phrynopus laplacai.—BOLIVIA: *La Paz:* 50 km NE La Paz, KU 154555–59; 3 km W Pongo, 3400 m, IBN/UNC 1251.6 (cleared and stained skeleton).

Phrynopus montium.—PERÚ: *Junín:* Cascas, MCZ 24352 (2 specimens, one a cleared and stained skeleton).

Phrynopus nanus.—COLOMBIA: *Santander:* Paramo de la Rusia, USNM 150643.

Phrynopus parkeri.—PERÚ: *Piura:* summit of cordillera between Chanchaque and Huancabamba, 3100 m, KU 135278–305, 135306 (cleared and stained skeleton), 135307–11.

Phrynopus peraccai.—ECUADOR: *Napo:* Papallacta, 3110 m, MIZ 820, USNM 164397; 1 km W Papallacta, 3155 m, KU 111430, USNM 160944 and 160950 (cleared and stained skeletons), 160954–59, 160961, 160966–68, 164398; 4 km W Papallacta, 3300 m, KU 117795–96, 118137 (cleared and stained skeleton); Laguna Papallacta, 3350 m, KU 109171.

Phrynopus pereger.—PERÚ: *Ayacucho:* Ccarapa, below Tambo on Ayacucho–Valle del Apurímac road, 2460 m, LSUMZ 26124–31; Huanhuachayocc, 1650 m, LSUMZ 26100; Mitupucuru, 2425 m, LSUMZ 26115–16; between Mitupucuru and Yuaccyacu, LSUMZ 26101–10, KU 151907 (cleared and stained skeleton), 151908–09; Yuraccyacu on Tambo–Valle del Apurímac trail, 2650 m, KU 151906 (cleared and stained skeleton), LSUMZ 26117–23, 26255.

Phrynopus peruanus.—PERÚ: *Junín:* Maraynioc, UMMZ 89477(2).

Phrynopus peruvianus.—PERÚ: *Cuzco:* N slope Abra Acanacu, 27 km NNE Paucartambo, 3450 m, KU 138919–25, 138926 (cleared and stained skeleton) 138927–35; 29 km NNE Paucartambo, 3400 m, KU 138917, 138936–64; 31 km NNE Paucartambo, 3270 m, KU 138968–69 (cleared and stained skeletons), 138970–78. *Puno:* near Juliaca, AMNH 14526, and one uncataloged cleared and stained skeleton.

Phrynopus simonsii.—PERÚ: *Cajamarca:* paramo, ca 8 km E Cajamarca, 3000 m, BMNH 1947.2.15.43–44.

Phrynopus wettsteini.—PERÚ: *? Amazonas:* Untuaro or Pongo, 2000 m, BMNH 1932.4.30.1–2, 1932.4.30.3 (cleared and stained skeleton), NMW 15846.1–2.

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